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AgriSciences**

Parentage in Social Ungulates

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Declaration

I hereby declare that I have done this thesis entitled “Parentage in Social Ungulates” independently, all texts in this thesis are original, and all the sources have been quoted and acknowledged by means of complete references and according to Citation rules of the FTA.

In Prague April 16, 2021

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Ema Cetkovská

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Abstract

Ungulates display a wide range of complex mating systems characterized by a multitude of factors, including the number of mating partners and territoriality. Sexual selection, the variability of reproductive success among individuals, is caused by various mechanisms, some of which are observable, while others, such as sperm competition and cryptic female choice, occurring in the female reproductive tract, are unperceivable. Consequently, mating behavior may not be reflected in parentage relations, and accurate parentage assignment may solely be obtained using molecular methods. The thesis is focused on the critically endangered Western Derby eland subspecies, with less than two hundred mature individuals remaining in Senegal, and the unthreatened common eland. Twelve microsatellite markers were used to assess paternity of putative sires of 41 Western Derby elands from the Senegalese semi-captive populations and 24 common elands kept in captivity at the University Farm Estate Lány. In addition to that, maternity was determined for 54 common elands at the University Farm Estate Lány. While the results of paternity assignment in the Western Derby elands correspond to predictions based on body condition, and the observational estimations of maternity in the common elands are generally accurate, mismatches between paternity predictions based on observations and the results obtained via molecular methods are more frequent in the common elands. This disparity in the accuracy of paternity predictions could be explained by the different management of the populations. While detailed composition of the Western Derby eland herds is recorded, information on the segregation of the common elands kept at the University Farm Estate Lány into the two parts of the facility, which determines the capacity of males to access females, is missing. Furthermore, the identity of the Western Derby elands is determined based on the permanent and unique stripe pattern, whereas the common elands are primarily identified using colorful ear tags, which are prone to falling off and consequently encumber paternity assignment.

Key words: parentage assignment, paternity, microsatellites, eland, *Taurotragus derbianus*, *Taurotragus oryx*

Contents

1. Introduction	1
2. Literature Review	3
2.1. Social Structure.....	3
2.2. Mating Systems	3
2.2.1. Monogamy	3
2.2.2. Polygamy	4
2.2.3. Promiscuity	5
2.2.4. Ungulate Mating Systems Based on Male Territoriality	5
2.2.4.1. Pair Territories.....	6
2.2.4.2. Polygynous Resource Territories.....	6
2.2.4.3. Lek Territories	7
2.2.4.4. Tending Bonds.....	9
2.2.4.5. Harems	10
2.3. Sexual Selection.....	11
2.3.1. Scrambles	12
2.3.2. Endurance Rivalry	13
2.3.3. Contests.....	13
2.3.4. Female Choice.....	14
2.3.5. Sexual Coercion.....	16
2.3.6. Infanticide	18
2.3.7. Induced Abortion.....	21
2.3.8. Sperm Competition.....	21
2.3.9. Sexual Selection and Sexual Dimorphism	23
2.4. Parentage and Paternity Assignment.....	24
2.5. Social Structure and Mating in Elands.....	27
2.5.1. Semi-captive Western Derby elands in Senegal.....	32
2.5.2. Captive common elands at the University Farm Estate Lány	34
3. Aims of the Thesis.....	36
4. Methods.....	37
4.1. Western Derby Elands.....	37

4.2.	Common Elands.....	37
4.2.1.	DNA Extraction.....	37
4.2.2.	Polymerase Chain Reaction (PCR).....	37
4.2.3.	Fragmentation Analysis	39
4.2.4.	Data Analysis	39
5.	Results	40
5.1.	Western Derby Elands.....	40
5.2.	Common Elands.....	41
6.	Discussion	44
7.	Conclusions	49
8.	References	51

List of tables

Table 1: Polymerase chain reaction protocol	38
Table 2: Composition of primer mixes E1 and E2	38
Table 3: List of sampled common elands.....	II (Appendices)
Table 4: Results of paternity assignment in Western Derby elands	V (Appendices)
Table 5: Results of paternity assignment in common elands	VII (Appendices)
Table 6: Results of maternity assignment in common elands	VII (Appendices)

List of the abbreviations used in the thesis

bp	base pair
DNA	deoxyribonucleic acid
ET	ear tag
FTA CZU	Faculty of Tropical AgriSciences, Czech University of Life Sciences Prague
ID	identification number
ITSA	Institute of Tropical and Subtropical Agriculture
IUCN	International Union for Conservation of Nature
PCR	polymerase chain reaction

1. Introduction

A wide array of complex social interactions and mating systems is observed in ungulates (Gosling 1986; Clutton-Brock 1989; Clutton-Brock 2016; Bowyer et al. 2020). Mating systems have traditionally been assessed exclusively based on behavioral observations (Hughes 1998), however, the discovery of genetic methods revealed the inaccuracy of such approach. Molecular analysis demonstrated that parentage does not always mirror mating behavior, since sires may be achieved by alternative strategies, which remain unperceived (Coltman et al. 1999; Mooring & Penedo 2014; Clutton-Brock 2016). In addition to that, male reproductive success may be influenced by sperm competition and cryptic female choice, which occur in the female reproductive tract and cannot therefore be observed (Parker 1970; Birkhead 1998; Simmons 2001). In the cases where differences between behavioral and genealogical relationships occur, genetic methods serve as the sole tool to acquire accurate parentage assignment (Coltman et al. 1999).

The practical part of the thesis is centered on the Derby eland (*Taurotragus derbianus*), specifically the Western Derby eland subspecies (*Taurotragus derbianus derbianus*), and the common eland (*Taurotragus oryx*). Both species belong to the *Tragelaphini* tribe (Castelló 2016), and they are the largest antelopes found in Africa (Pappas 2002). On the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, common elands are attributed the status “Least Concern”, with a stable population trend and the estimated number of living mature individuals between 90,000 and 110,000. They are found in seventeen countries throughout sub-Saharan Africa, from South Sudan to South Africa (IUCN 2016). Contrarily, Western Derby elands are classified as “Critically Endangered” on the IUCN Red List of Threatened Species, having a decreasing population trend. Only 120-150 mature individuals are remaining (IUCN 2017), and they are exclusively found in Senegal. The only known wild population of Western Derby elands is located in the Niokolo Koba National Park in southeastern Senegal, and several herds of semi-captive Western Derby elands are established in the Bandia Reserve and the Fathala Wildlife Reserve in the western part of the country (Brandlová et al. 2020).

The thesis is focused on parentage assignment in the herds of Western Derby elands in the Senegalese reserves and in the common elands kept at the University Farm Estate Lány. Parentage relations of Western Derby elands in the Senegalese semi-captive populations are determined based on behavioral observations and male body condition, and they are reported in the annually published studbook (Brandlová 2021, pers. comm.). In the captive population of common elands kept at the University Farm Estate Lány, parentage assignment is performed using the observational data obtained by the eland keeper, and they are recorded in regular written reports (Neradilová 2021, pers. comm.). Since parentage assessment based on observations may be inaccurate, verification using molecular methods is desirable.

2. Literature Review

2.1. Social Structure

Various social structures are observed in ungulates, ranging from solitary living to formation of large herds. Character of habitat, risk of predation, availability of natural resources, and availability of mates are recognized as the principal determinants of the adopted type of social organization (Bowyer et al. 2020).

According to Davies et al. (2012), grouping reduces predation risk, improves defense against predators, and enables rapid exchange of information regarding food sources or potential danger. Furthermore, aggregation of individuals enhances thermoregulation (Clutton-Brock 2016; Majolo & Huang 2018), provides protection against insect attacks (Hamilton 1971), and helps gain access to mating partners (Majolo & Huang 2018). However, grouping is associated with a multitude of disadvantages, such as greater competition among individuals, facilitation of disease transmission (Davies et al. 2012), and enhancement of aggression (Isvaran 2007). Bowyer et al. (2020) concluded that structured groups are established and maintained as long as the benefits of such arrangements exceed the costs.

2.2. Mating Systems

Degree of sociality is, along with environmental and morphological aspects, an important factor influencing which mating strategy is implemented (Bowyer et al. 2020). The term “mating system” comprises the tactic used to acquire mates, the total number of mates, and the extent to which an individual provides parental care to its offspring (Hughes 1998; Davies et al. 2012). Mating systems are commonly categorized based on the number of mating partners (Emlen & Oring 1977; Vanpé 2005), as monogamous, polygamous, or promiscuous (Davies et al. 2012).

2.2.1. Monogamy

Davies et al. (2012) defined monogamy as a strategy where one male and one female exclusively mate with each other during at least one breeding season, voluntarily or

forcibly forgoing other mating opportunities. However, Clutton-Brock (2016) stated that extra-pair mating may be observed in monogamously living species and consequently identified three subtypes of monogamy, based on the evidence for the absence of reproduction outside of the established pair. In social monogamy, two breeding adults are seen living in pairs (Lukas & Clutton-Brock 2013; Clutton-Brock 2016), whereas in sexual monogamy, no extra-pair mating is observed. Genetic monogamy describes a situation where the absence of breeding with other individuals is genetically proven (Clutton-Brock 2016).

Monogamy can also be approached from the female perspective, and a distinction of long-term and serial monogamy may be made. In long-term monogamous relations, a mating bond between a female and a male is maintained for the majority of their lifespans, whereas in serial monogamy, the female consecutively creates bonds with multiple males, each only lasting for a limited time period (Clutton-Brock 1989).

Monogamous mating systems have been observed in less than 3% of mammalian species (Kleiman 1977), with their occurrence in ungulates being relatively rare in comparison to other mammals (Lukas & Clutton-Brock 2013; Clutton-Brock 2016). Monogamy has been reported in several antelope species, including Kirk's dik-dik (*Madoqua kirkii*; Kranz 1991; Brotherton et al. 1997) and klipspringer (*Oreotragus oreotragus*; Dunbar & Dunbar 1980; Tilson 1980).

2.2.2. Polygamy

Davies et al. (2012) defined polygamy, comprising polygyny and polyandry, as a strategy where breeding with multiple mates is observed in an individual of either sex. In polygyny, males mate with more than one female, whereas females restrict their reproduction to solely one male. In polyandry, the situation is reversed, with females having multiple mates and males breeding with only one female (Vanpé 2005). Shuster and Wade (2003) equally mentioned polygynandry, characterizing it as a mating system where both males and females have multiple partners. The authors also highlighted the inconsistency in the usage of terminology regarding mating systems, stating that the cases where both partners mate with more than one individual are sometimes encompassed in the terms “polygyny” and “polyandry” (Shuster & Wade 2003).

Clutton-Brock (2016) further distinguished range-guarding and site-guarding subtypes of polygyny. In range-guarding polygyny, males defend territories containing home ranges of multiple females or their herds. Site-guarding polygyny refers to males guarding territories smaller than female home ranges, with common occurrence of natural resources. Passing by females are drawn to such areas and later mate with the guarding male (Clutton-Brock 2016). Emlen and Oring (1977) referred to these territory guarding subtypes of polygyny as resource defense polygyny, differentiating them from female defense polygyny, where males guard females directly. Such strategy is adopted if female ranges are unsuitable for defense due to their largeness and female aggregations are stable (Clutton-Brock 2016).

Most ungulate species engage in polygynous mating systems (Vanpé 2005), with resource defense polygyny being the most commonly adopted strategy among antelopes (Gosling 1986). White-tailed deer (*Odocoileus virginianus*) is traditionally regarded as polygynous (Neuman et al. 2016), however, the occurrence of multiple paternity implies that females do not restrict their reproduction to solely one male (DeYoung et al. 2002; Neuman et al. 2016). Similarly, Mooring and Penedo (2014) refer to American bison (*Bison bison*) as polygynous, although females were found to copulate with multiple males during one season. Briefer et al. (2013) stated that polyandrous behavior was observed in female fallow deer (*Dama dama*), despite defining the species as highly polygynous.

2.2.3. Promiscuity

Davies et al. (2012) defined promiscuity as a strategy, where both male and female mate with multiple partners over the course of one breeding season. It is characterized by the absence of a long-term bond between mating individuals (Clutton-Brock 1989). The occurrence of promiscuity in ungulates is scarce, compared to other mating systems (Vanpé 2005). Topi antelope (*Damaliscus lunatus*; Bro-Jørgensen 2007) and Soay sheep (*Ovis aries*; Preston et al. 2003) were found to be promiscuous.

2.2.4. Ungulate Mating Systems Based on Male Territoriality

Höglund and Alatalo (1995) disfavored the categorization of mating systems based on the number of partners, remarking that it disregards important factors influencing reproductive strategies, such as territoriality, bonds between mates, and parentage.

Furthermore, this method of classifications is not applicable to all mating strategies, and it may produce inconsistent results when used by different authors (Höglund & Alatalo 1995).

Bowyer et al. (2020) took a different approach, classifying ungulate mating systems according to the territoriality of males. Pair territories, polygynous resource territories, and lek territories are types of territorial breeding strategies, while nonterritorial tactics include tending bonds and harems. Despite being based exclusively on male behavioral patterns, this categorization reflects the comportment of females and female choice, which significantly contribute to the character of mating systems (Bowyer et al. 2020).

2.2.4.1. Pair Territories

A pair territory is inhabited by one monogamous male and one monogamous female, and it is commonly defended against other individuals. It is essential for the guarded area to encompass resources required by adults and their offspring (Bowyer et al. 2020). Gosling (1986) thus referred to this mating strategy as “resource defense monogamy”. A monogamous system is established if the size of female home ranges exceeds that of male ranges or territories (Clutton-Brock 2016). The largeness of female ranges does not allow males to defend more than one female (Davies et al. 2012). Pair territories are observed in multiple antelope species, including klipspringer (*Oreotragus oreotragus*; Dunbar & Dunbar 1980) and Kirk’s dik-dik (*Madoqua kirkii*; Gosling 1986; Kranz 1991; Brotherton et al. 1997), as well as several cervids (Bowyer et al. 2020).

2.2.4.2. Polygynous Resource Territories

Polygynous resource territories are commonly defended by a single male (Bowyer et al. 2020), and their size surpasses that of ranges occupied by females (Davies et al. 2012). Females are drawn to the area by the presence of natural resources (Bowyer et al. 2020); the proportions of the territory and the extent to which female home ranges overlap determining the total number of females (Clutton-Brock 2016). This strategy is likely to be adopted in areas where the accumulation of high-quality food sources that last for multiple seasons encourages long-term aggregation of females. Synchronized and relatively short estrus also promotes territory guarding, as males gain mating opportunities by defending resources demanded by females during breeding period.

Furthermore, this tactic is beneficial to males because it is less costly than following females, and the knowledge of terrain provides an advantage in case of pursuit by predators (Gosling 1986). Polygynous resource territories have been observed in guanaco (*Lama guanicoe*; Marino et al. 2016), fallow deer (*Dama dama*; Clutton-Brock et al. 1988), topi (*Damaliscus lunatus*) and puku (*Kobus vardonii*) antelopes (Balmford et al. 1992), and black lechwe (*Kobus leche smithemani*; Nefdt & Thirgood 1997).

2.2.4.3. Lek Territories

Leks are defined as aggregations of males, where each individual guards a small mating area with proportions only attaining a few meters (Davies et al. 2012). The absence of natural resources is the main factor differentiating lekking areas from resource-based territories (Bowyer et al. 2020). Estrous females enter leks in order to mate with males, leaving the area shortly thereafter to rejoin their herds of origin. On the contrary, males occupy the territory for a longer period of time, attempting to attract multiple females. The lekking strategy is also characterized by the absence of paternal care (Höglund & Alatalo 1995). Despite being a relatively rare mating system (Isvaran 2005), lekking has been observed in several ungulate species (Davies et al. 2012; Clutton-Brock 2016). Most ungulate leks are occupied by five to two hundred individuals (Clutton-Brock et al. 1993).

Bradbury and Gibson (1983) distinguished classical leks and exploded leks based on the distance between them and the degree of aggregation of males. Classical leks are situated further apart and are characterized by a high density of males. Contrarily, the distance between exploded leks is shorter, and males are less densely dispersed (Bradbury & Gibson 1983). However, a different usage of the term “classical lek” was employed in Clutton-Brock (1989), indicating an aggregation of males visited by estrous females solitarily or in small groups. This specification was used since the term “lek” was also applied to the situation where areas of clustered male territories are frequently traversed by large female herds. The females in estrus stay on the lek to mate, while the rest of the group moves on (Clutton-Brock 1989).

In many species of ungulates, mating areas on leks are occupied by only a small proportion of males (Isvaran 2005), typically older and dominant ones. Younger and subordinate individuals hold bigger territories containing natural resources in areas

between leks. The number of mating attempts increases towards the center of the lek, resulting in the less dominant and younger males being rarely successful (Clutton-Brock 2016). These males have been observed using alternative mating tactics, such as breeding with females in mixed-sex herds or intrusion into areas guarded by other males in an attempt to mate with females inhabiting the territory (Isvaran 2005). Bradbury and Gibson (1983) suggested that the advent of such strategies stems from the uneven distribution of reproductive success.

Lekking strategies display great complexity (Bradbury & Gibson 1983), and multiple plausible hypotheses explaining their evolution have been proposed and examined (Höglund & Alatalo 1995). Aggregation on leks may provide reduced predation risk for both males and females (Gosling 1986; Höglund & Alatalo 1995), enhance sharing of information among individuals or increase male reproductive success (Höglund & Alatalo 1995). The establishment of leks might equally be induced by the patchiness of habitat (Gosling 1986; Höglund & Alatalo 1995). Additionally, Davies et al. (2012) mentioned that aggregation of males could enable females to exercise mate choice more thoroughly.

Hotspot, hotshot, and black hole models have also been proposed as potential explanations for the evolution of lekking strategies. Hotspots are defined as undefendable areas where natural resources, such as water or food, are accumulated (Höglund & Alatalo 1995) or where multiple female home ranges overlap, resulting in a higher concentration of females (Bradbury et al. 1986; Höglund & Alatalo 1995). Since male distribution tends to mirror the dispersion of females (Davies et al. 2012), male aggregations are likely to form at such places (Höglund & Alatalo 1995). The hotshot model is based on the preference of females for certain males and their aversion towards others. The proximity of a favored male might benefit the less preferred ones, increasing their mating success. This advantage of male accumulation could have contributed to the evolution of leks (Beehler & Foster 1988; Höglund & Alatalo 1995).

The black hole model estimates that females seek safe and harmless mating, rather than a specific type of males (Höglund & Alatalo 1995). Younger and less experienced individuals are more likely to be avoided by females (Clutton-Brock et al. 1993; Andersson 1994; Clutton-Brock 2016), due to their inability to ward off competitors who

might sexually harass females or interrupt mating (Andersson 1994; Clutton-Brock 2016). Females react to this risk by leaving the territory guarded by an inexperienced male without mating and proceeding to other areas in order to search for a more suitable partner. Nevertheless, if no appropriate male is accessible, females will eventually mate with the one situated closest to them, regardless of the age and experience. It has thus been suggested that clustered males are likely to attain greater mating success than solitary ones, even if certain individuals from the aggregation are rejected (Höglund & Alatalo 1995).

Opinions regarding the evolution of leks vary considerably among authors, and a consensus is yet to be reached (Clutton-Brock 2016). Due to the extreme variability of lekking systems, it is unlikely for a single idea to provide universal explanation of their development. Since various lekking species differ significantly in terms of ecology, life history, and habitat, it is possible for the factors influencing the evolution of leks to be unique for every species (Höglund & Alatalo 1995). Gosling (1986) concluded that the identification of factors leading to male aggregation, and other lekking precursors might be of a greater importance than the attempts to find a universal explanation for the evolution of leks.

The occurrence of lek territories has been reported in fifteen mammalian species (Bowyer et al. 2020), which makes this mating system relatively rare (Nefdt & Thirgood 1997). Lekking mating strategies have been found in fallow deer (*Dama dama*; Clutton-Brock et al. 1988), sika deer (*Cervus nippon*; Bartoš et al. 2003), Uganda kob (*Kobus kob thomasi*; Leuthold 1966; Balmford & Turyaho 1992; Deutsch 1994), Kafue lechwe (*Kobus leche kafuensis*; Schuster 1976; Nefdt & Thirgood 1997), and topi (*Damaliscus lunatus*; Gosling & Petrie 1990).

2.2.4.4. Tending Bonds

Tending bonds are traditionally defined as mating systems where a dominant male guards only one receptive female at a time with no occurrence of territory establishment (Bowyer et al. 2020). Although dominant males adopt aggressive behavior towards other males in order to protect the guarded females, they never restrict the estrous females in their movement. Since subordinate males are unable to defend receptive females, they

commonly engage in alternative mating tactics, such as blocking or coursing (Hogg & Forbes 1997).

The aim of blocking is to restrain the movements of females until estrus is reached, so that females are kept away from dominant males and thus unable to mate with them. In coursing, subordinate males endeavor to forcibly gain temporary access to females guarded by dominant males. This strategy requires great physical agility, since females adopt various tactics, such as traversing dense vegetation or entering unfavorable terrain, in an attempt to decelerate the pursuing males and avoid mating with them. Copulation resulting from coursing is thus uncooperative, whereas the engagement of females in tending and blocking mating is deliberate (Hogg & Forbes 1997).

Clutton-Brock (2016), who referred to the tending mating system as “female-guarding polygyny”, stated that tending commonly occurs in species where females live solitarily or in small groups, their movement is unpredictable, and the density of their distribution is low. Bowyer et al. (2020) stated that the formation of tending bonds is the primary mating system in ungulates inhabiting mountainous, forested, or woody areas. It has been documented in Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*; Hogg & Forbes 1977), barren-ground caribou (*Rangifer tarandus groenlandicus*; Lent 1965), white-tailed deer (*Odocoileus virginianus*; Newbolt et al. 2017; Foley et al. 2018), American bison (*Bison bison*; Bowyer et al. 2007), and common eland (*Taurotragus oryx*; Underwood 1975).

2.2.4.5. Harems

Harem mating systems, also termed “group-guarding polygyny”, are characterized by a single male defending a herd of females from rival individuals (Clutton-Brock 2016). Subordinate males, who are incapable of guarding a harem, are traditionally located in proximity and adopt sneaking strategies in an attempt to mate with member females of the nearby harems (Bowyer et al. 2020). Clutton-Brock (1989) identified two possible ways of harem formation based on the risk of inbreeding. If the age of females at first reproduction exceeds the length of harem tenure by the dominant male, inbreeding is prevented, and harems may be composed of related females. However, in case of high

risk of inbreeding occurrence, females leave their herds of origin and join harems that are not formed by related individuals (Clutton-Brock 1989).

Permanent or seasonal harems may be established, depending on the timing and synchronicity of estrus in females. Permanent harems are defended by dominant males for the entirety of their reproductive lives, since females become receptive nonconcurrently and rather unexpectedly. On the contrary, seasonal harems are formed if all member females of the harem come into estrus predictably, at a particular time of the year (Davies et al. 2012). Bowyer et al. (2020) stated that multimale harems, consisting of one dominant male, several subordinate males, and a number of females, may occur. The dominant male may benefit from the presence of subordinate males, as they ward off potential intruders and thus contribute to the integrity of the harem. Although subordinate males rarely get the opportunity to mate within the harem due to being chased off by the dominant male, they might eventually inherit the harem (Stevens 1990). Harem mating systems are observed in several ungulate species, such as red deer (*Cervus elaphus*; Clutton-Brock 1985), feral horse (*Equus caballus*; Stevens 1990), saiga antelope (*Saiga tatarica tatarica*; Milner-Gulland et al. 2003), and common eland (*Taurotragus oryx*; Underwood 1975).

2.3. Sexual Selection

Andersson (1994) defined sexual selection as the variability in reproductive success among individuals, issued from the differences in the development of traits that influence their ability to gain breeding opportunities and mate successfully. Although attention has been predominantly drawn to intrasexual competition for partners and mate choice (Clutton-Brock & Parker 1995; Andersson & Iwassa 1996), multiple mechanisms of sexual selection have been observed (Andersson 1994).

Even though sexual selection can be targeted at both sexes, it is typically stronger in males (Trivers 1972; Davies et al. 2012). Several explanations have been proposed, including anisogamy and variation in paternal care (Andersson 1994). Immobile female gametes are generated in small amounts, whereas males produce a large number of motile gametes (Bateman 1948; Davies et al. 2012). The excess of male gametes and the supreme energy

investment required for egg production result in sexual selection favoring females (Andersson 1994). This preference is equally supported by the fact that females traditionally display greater engagement in providing parental care than males, which is associated with energetic and temporal costs (Davies et al. 2012). Trivers (1972) included both gamete production and parental care in the term “parental investment”, defined as any action increasing the chances of progeny survival while limiting the capacity of an individual to sire more offspring.

The variation in the strength of sexual selection can equally be explained by operational sex ratio, which is characterized as the mean proportion of females capable of being impregnated to sexually active males at a given point in time (Emlen 1976). Operational sex ratio is influenced by the distribution of the less numerous sex in time and space, the length and synchronicity of estrus, the duration of male sexual activity period (Emlen & Oring 1987), and the mortality rate of both sexes (Andersson 1994). If females are outnumbered by males, sexual selection is likely to be stronger in males. In case of the polar opposite situation, which is less commonly observed, an enhancement of the power of sexual selection in females is expected. Moreover, an increase in the disbalance between the number of males and females indicates greater variance in reproductive success of both sexes (Emlen & Oring 1987).

Andersson (1994) identified scrambles, endurance rivalry, contests, mate choice, and sperm competition as principal mechanisms of sexual selection. The list was further expanded by the addition of infanticide, induced abortion, and coercion (Andersson & Iwassa 1996), with the latter being particularly emphasized by Clutton-Brock and Parker (1995). Andersson and Iwassa (1996) concluded that a multitude of these mechanisms is likely to occur simultaneously, rendering the determination of their respective significance difficult.

2.3.1. Scrambles

Scrambling encompasses strategies that enable individuals to find mating partners faster than their adversaries (Andersson & Iwassa 1996), consequently augmenting their reproductive success (Andersson 1994). This can be achieved by an early maturation of males in comparison to females, which provides males with additional time to search for

potential partners. Certain characteristics, such as increased mobility, great memory, or well-developed sensory organs, facilitate and accelerate the localization of mates (Andersson & Iwassa 1996). Advanced searching behavior is especially crucial in species with high and unpredictable dispersal of females (Trivers 1972).

The tending bond mating system employed by white-tailed deer (*Odocoileus virginianus*) is considered to be a form of scramble competition (Foley et al. 2018), since subordinate males invest a significant amount of time in the search for estrous females. They may thus locate a receptive female faster than dominant males, which results in them siring her offspring while avoiding direct confrontation with the superior male (Jones et al. 2011).

2.3.2. Endurance Rivalry

Endurance of males has a significant impact on the duration of their sexual activity and the time they spend on mating areas (Andersson 1994; Andersson & Iwassa 1996). Physical condition of an individual is closely associated with their endurance, and males in a better shape are thus capable of sustaining demanding activities related to reproduction for a longer time period than males in poor condition (Higham et al. 2011). Since males with traits enhancing endurance gain more opportunities to mate with females and display great reproductive success, such characteristics are favored by sexual selection (Andersson 1994).

Jones et al. (2011) identified endurance rivalry as a plausible explanation for seasonal dominance shifts in white-tailed deer (*Odocoileus virginianus*). Subordinate males were seen to gain more mating opportunities later in the breeding season, when the originally dominant individuals displayed poorer condition due to weight loss sustained during intensive reproductive efforts. Initially smaller dominant males were more prone to being displaced by subordinate animals, in comparison to those who outweighed their rivals considerably (Jones et al. 2011).

2.3.3. Contests

Males attempt to gain access to receptive females or resources related to reproduction through engagement in contests (Andersson 1994; Clutton-Brock 2016), which are characterized as physical fights among males or displays of the individual's strength to

potential rivals (Andersson 1994). Such intermale competition has led to the selection for strength, which is commonly associated with large body size (Andersson & Iwassa 1996; Clutton-Brock 2016), as well as to the selection for weapons, ornaments, and other signals indicating strength (Andersson 1994).

Physical fights are relatively common among mammals, and numerous ungulate species have been reported to engage in such combats (Clutton-Brock 2016). A significant variability of contest strategies has been observed in different species (Trivers 1972; Clutton-Brock 2016), with smaller animals commonly favoring stabbing or biting, contrarily to larger species which preferentially adopt pushing tactics, requiring a great body mass (Clutton-Brock 2016). The character of fights is equally influenced by spatial and temporal distribution of females, as well as the predictability of their position in time and space. Physical conflicts among males are encouraged in situations where females become receptive synchronously. In addition to that, males are likely to become especially aggressive when located at places where estrous females are expected to aggregate (Trivers 1972). Furthermore, violent fights are more frequently observed in species where multiple females are guarded by one male, in comparison to those where a male defends solely one or two females (Clutton-Brock 2016).

Contests are associated with numerous disadvantages to males, including an elevated risk of injury and energetic costs of weaponry maintenance. Moreover, individuals engaging in fights are temporarily incapable of protecting females and might thus lose them (Clutton-Brock 2016). Due to these costs, males use rivals' visual, vocal, and olfactory displays to assess their strength (Clutton-Brock 2016), and decide to avoid physical combats with them if they are unlikely to come out victorious (Andersson 1994; Clutton-Brock 2016). Resident males use their weaponry and ornaments to demonstrate their strength to intruders, vocal displays to signal their presence to potential adversaries, and olfactory displays to deter them (Clutton-Brock 2016).

2.3.4. Female Choice

Clutton-Brock (2016) defined female choice as a situation where female mating preference for certain males is observed, regardless of whether the mating results in conception or not. Female choosiness is considered to be an important factor shaping the

character of mating systems (Bowyer et al. 2020). Despite its significance being primarily associated with lek breeding systems, where it is particularly apparent, female choice is mirrored in the majority of mating systems (Clutton-Brock 2016).

The adoption of female choice is associated with a number of both genetic and non-genetic benefits (Andersson 1994). Genetic advantages comprise the impact of mate choice on offspring genotypes, resulting in the enhancement of their fitness, while having no consequence to the females. Contrarily, non-genetic advantages, equally termed “direct benefits”, affect females themselves, increasing the probability of their survival and improving their fecundity (Clutton-Brock 2016).

Supreme genetic qualities of progeny and attractiveness of male offspring are the principal concepts encompassed in the genetic benefits of female choice (Clutton-Brock 2016). Zahavi (1975) suggested that females show preference for individuals with body features that diminish their chances of survival. Males possessing such traits are likely of great fitness, as they are capable of prospering despite their handicap. Although individuals with no disadvantageous characteristics are presumably fitter, their quality is not observable and thus cannot be the subject of female choice (Zahavi 1975). Fisher (1930) proposed the idea of female preference for attractive males, as mating with such individuals is likely to result in male offspring with traits favored by females. These descendants have a higher chance of being chosen as mating partners, compared to other individuals, potentially resulting in a greater reproductive success (Fisher 1930).

Clutton-Brock (2016) identified risk reduction, fecundity enhancement, social advantages, and offspring protection as principal direct benefits of female choice. Females show preference for dominant males as mating with them is less likely to be interrupted by subordinate individuals, and the risk of sustaining life-threatening injuries is thus diminished. Mate choice can equally ensure superior protection against predators (Andersson 1994; Clutton-Brock 2016). In addition to that, copulations with high quality males prevent parasite and disease transmission (Andersson 1994). Dominant males guarding territories of supreme quality also tend to tolerate their partners' presence in proximity. This provides the social advantage of the access to important natural resources located within the territories to females mating with such males (Clutton-Brock 2016).

Preference for fertile males and avoidance of those visibly weak and undernourished reduces the chances of infertile mating and consequently contributes to the improvement of female fecundity (Trivers 1972; Andersson 1994). Males of poor health also have diminished chances of survival, and mating with them is therefore associated with the risk of the absence of paternal care in case of the male's death (Trivers 1972). Furthermore, breeding with dominant males is beneficial due to their capacity of protecting their progeny from infanticide (Clutton-Brock 2016).

Aside from having genetic and non-genetic benefits to females, female choice positively impacts the reproduction of males, providing them with the opportunity to demonstrate their qualities, which might in turn help attract females possessing superior characteristics. Nevertheless, numerous disadvantages for both sexes pertain to female choosiness. Males sustain temporal costs and energy loss as a consequence of advertising their qualities (Zahavi 1975). Females suffer similar costs while examining potential mating partners in search for the most suitable one, and they are concurrently prone to harassment by subordinate males attempting to mate with them (Clutton-Brock 2016). Kokko et al. (2003) also mentioned forgone mating opportunities stemming from the rejection of certain males among the costs of female choice. Moreover, paternal care for offspring is likely to be limited due to the costliness of the advertising process, leaving females with little help from their mating partners (Zahavi 1975).

The disadvantageousness of female choice to males resulted in the development of counterstrategies adopted by males in an attempt to maximize their gains. Individuals may increase their temporal and energetic investment into mating with females that find them desirable in order to enhance their chances of reproductive success, while forgoing other breeding opportunities. However, males can equally engage in the polar opposite strategy, mating with as many partners as possible and concurrently reducing the effort put into each copulation. Coercive tactics may also be adopted, completely avoiding female choice and sparing males from potential rejection (Glover & Crowley 2017).

2.3.5. Sexual Coercion

Smuts and Smuts (1993) defined sexual coercion as any violent action adopted by males to increase the likelihood of mating with a fertile female while limiting the probability of

the female breeding with other individuals, or threats of such comportment. Clutton-Brock and Parker (1995) distinguished forced copulation, harassment, and intimidation as three types of sexual coercion. Smuts and Smuts (1993) considered infanticide as a subtype of coercion, nevertheless, Andersson and Iwassa (2004) listed them as two separate mechanisms of sexual selection.

Forced copulation comprises situations where males use their physical characteristics, such as strength or speed, to violently gain mating opportunities. This strategy leads to conflicts between both sexes, as females might benefit from rejecting certain males and waiting for more favorable ones, whereas males gain the most by mating immediately with the chosen female, since every additional mating may increase their reproductive success. Coming out victorious is thus crucial to males, which led to the development of strong selection for physical traits enabling males to force copulations. Victory is vital to females especially if the male is genetically undesirable or mating with such individual would provoke violent behavior and harassment from other males (Clutton-Brock & Parker 1995). In such situations, females show a great deal of resistance (Glover & Crowley 2017).

Males may equally gain mating opportunities by adopting harassment strategies, which consist of numerous repeated attempts to copulate with a female. Such behavior results in the female accepting to mate, even if the male is not desirable, in order to prevent sustaining injuries by recurrent courtship. It is especially beneficial for the female to surrender in situations where males have significantly larger proportions than females and could consequently cause serious harm to females, or if females that have already bred are less prone to male harassment than those who have not (Clutton-Brock & Parker 1995). Nevertheless, estrous females are commonly first spotted by young and subordinate males that lack experience and are unable to ward off males attempting to interrupt copulation. The risk of injury is elevated, and genetic benefits are limited in case of such mating, which results in females being reluctant to submit to male violence (Clutton-Brock 2016).

Intimidation strategies are characterized by the adoption of violent behavior and punishment in order to induce fear in females. Females are punished for their reluctance

to mate with the male or for favoring other individuals and breeding with them. As a result, females are willing to copulate with the male in an attempt to prevent the violence that might otherwise be targeted at them and potentially lead to serious injuries. Intimidation tactics are frequently observed in large groups comprising several males and multiple females, since males are unable to easily ensure exclusive access to females in such situations. It is thus beneficial to them if females fear the consequences of seeking mating opportunities with other individuals. On the contrary, few cases of intimidation have been reported in monogamous societies and in one-male harems (Clutton-Brock & Parker 1995).

In tending bond mating systems, the ability to guard receptive females is restricted to dominant males. Subordinate individuals adopt coursing strategies, which consist of approaching the tending pair and inducing a combat with the dominant male, attempting to separate him from the female. If successful, the subordinate male proceeds to chase the female and forces her to copulate. This strategy has been observed in bighorn sheep (*Ovis canadensis*; Hogg 1984; Pelletier et al. 2006). Similarly, juvenile males attempt to chase estrous females present on leks defended by older males in fallow deer (*Dama dama*; Clutton-Brock et al. 1992). Coercive strategies are equally adopted by wild horses (*Equus caballus*; Berger 1983), reindeer (*Rangifer tarandus*; Holand et al. 2006), and Kafue lechwe (*Kobus leche kafuensis*; Nefdt & Thirgood 1997).

2.3.6. Infanticide

Mock (1984) defined infanticide as any comportment of an individual that contributes to the death of an unborn or recently born young of the same species. In order to be classified as infanticide, such behavior must have immediate lethal consequences on the victim, which excludes any actions causing death in a distant future (Mock 1984). Despite regarding such definition as conventional, Hrdy and Hausfater (1984) showed preference for a more expansive explanation of infanticide as any behavior of an individual leading to the reduction of care for young of the same species and their death. Palombit (2015) proposed an even broader definition, classifying infanticide as any comportment with a lethal impact on conspecific infants. He also suggested that the complexity of the subject is mirrored in this variability of definitions (Palombit 2015).

Although lethal encounters may occur between related individuals, the vast majority of cases reported in mammals lack any genetic relations between aggressors and victims (Hrdy & Hausfater 1984; Mock 1984). Infanticide shows great variability, since it can be adopted by both males and females (Hrdy & Hausfater 1984; Clutton-Brock 1998), and it has been observed in a great number of different social systems and arrangements (Palombit 2015) across a large spectrum of animal species. Although its occurrence is relatively common in certain mammals, such as primates and rodents, it has only rarely been reported in ungulates (Clutton-Brock 2016). In species where such aggressive behavior towards young individuals is adopted, infanticide accounts for the majority of infant deaths (Palombit 2015; Clutton-Brock 2016).

The evolution of infanticide has no universal explanation (Hrdy & Hausfater 1984; Palombit 2015), and numerous plausible hypotheses have been proposed. The oldest among them is the sexual selection hypothesis (Palombit 2015), which suggests that infanticide in males enhances their fitness and reproductive success. It is primarily targeted at young individuals highly dependent on maternal care (Clutton-Brock 2016), since their decease inhibits lactation in their mothers and accelerates their return into estrus, enabling male aggressors to mate with them and potentially sire offspring. Furthermore, prematurely terminated lactation likely ensures better condition of the female at the following mating, thus increasing reproductive success (Palombit 2015). Males adopting infanticide are commonly individuals immigrating into established social groups, attempting to kill the progeny of member males and gain opportunity to breed with the females (Hrdy & Hausfater 1984; Palombit 2015; Clutton-Brock 2016). Moreover, aggression towards infants also occurs during dominance rank changes within groups, with males aiming for higher positions in the hierarchy attacking offspring of their predecessors. The likelihood of infanticide development is elevated in situations where dominant males are numerous (Palombit 2015).

According to mate acquisition hypothesis, male infanticide is adopted because it helps males demonstrate their strength in comparison to other individuals. Females might consequently decide to join the stronger males and mate with them, thus increasing their reproductive success. Furthermore, infanticide diminishes fitness of adversaries, and killing male infants may eliminate potential future rivals. The evolution of male

infanticide can equally be explained by numerous additional benefits, such as the gain of access to natural resources or breeding areas. Moreover, human induced changes in habitat might contribute to the development of infanticide, or it could be an unintentional byproduct of male aggression (Palombit 2015).

While undoubtable advantages to males are issued from infanticide, females suffer great costs (Trivers 1972) and consequently develop strategies to prevent male aggression towards their offspring. Females might mate with multiple males or display unreliable signs of receptivity that do not reflect the timing of ovulation in an attempt to confuse males and prevent them from accurate paternity determination. Since males are unwilling to risk the death of their own progeny, they are less likely to resort to infanticide. Females might also adopt aggression towards intruding males, which is especially enhanced during gestation, lactation, or presence of the young (Palombit 2015; Clutton-Brock 2016). In addition to that, females attempt to keep at a significant distance from potentially infanticidal males (Palombit 2015) or prefer to mate with them if such action leads to infanticide prevention (Clutton-Brock 2016).

Male infanticide could equally promote female coalitions, since grouping increases the likelihood of detecting potential infanticidal males, and cooperative aggression towards them presumably has a greater impact (Palombit 2015; Clutton-Brock 2016). However, Clutton-Brock (2016) suggested that formation of large groups might attract potential intruders and thus be disadvantageous in some instances. Female avoidance of big herds, their transfer to smaller ones, or aggression towards females attempting to join the groups are likely to occur in such cases (Clutton-Brock 2016). Infanticide may also lead to female preference for strong and dominant males that are capable of providing protection against other infanticidal individuals (Palombit 2015; Clutton-Brock 2016). If such males are absent, females are likely to leave the herd and search for a different social group that would better fulfill their needs (Clutton-Brock 2016).

Infanticide rarely occurs in ungulates, with the majority of the cases being reported in equids (Král et al. 2019). Male infanticide has been seen in plains zebra (*Equus burchelli*; Pluháček & Bartoš 2000), Przewalski horse (*Equus przewalskii*; Ryder & Massena 1988), feral horse (*Equus caballus*; Duncan 1982), and red deer (*Cervus elaphus*; Bartoš &

Madlafousek 1994). A case of infanticide performed by two females was observed in white-lipped deer (*Cervus albirostris*; Král et al. 2019).

2.3.7. Induced Abortion

Induced abortion, also termed “pregnancy termination” (Palombit 2015), may be regarded as a method of sexual selection used by males (Andersson 2004; Andersson & Iwassa 2006), or as a female counterstrategy to infanticide (Labov et al. 1985; Palombit 2015; Clutton-Brock 2016; Eccard et al. 2017). Pregnant females might be subjected to sexual harassment or forced copulations by immigrant males, as well as other stress factors stemming from changes in social structure, resulting in the abortion of unborn offspring (Berger 1983). Males benefit from such situations, as fitness of their rivals is diminished, and the return of females to estrus is accelerated, enabling males to mate with them (Andersson 2004). Abortion may also be induced when social changes (Palombit 2015) and the appearance of unknown males present a risk of infanticide (Eccard et al. 2017). Clutton-Brock (2016) suggested that females are likely to prematurely terminate pregnancies if the chances of offspring survival of male aggression are slim. Berger (1983) concluded that the causes of induced abortion are unclear, and a multitude of factors presumably contributed to its evolution.

Induced abortion has been reported in wild horses (*Equus caballus*), where the appearance of an immigrant male resulted in an abortion in 90% of females that were less than six months pregnant. Eighty percent of these gravidity terminations were caused by forced copulation, with the remainder being supposedly induced by harassment or stress factors. However, older fetuses seem to be more likely to survive the introduction of a new male, compared to younger ones (Berger 1983).

2.3.8. Sperm Competition

Sperm competition is defined as a competition for the fertilization of female eggs that occurs among sperm of multiple males (Parker 1970; 1998) present simultaneously in the female reproductive tract at the site of fertilization (Simmons 2001). This strategy is associated with cryptic female choice (Birkhead 1998; Ball & Parker 2003). Similarities between male combats and sperm competition, as well as female mate choice and female

cryptic choice, have been observed, suggesting the existence of an analogy between precopulatory and postcopulatory processes (Eberhard 1996; Davies et al. 2012).

Mating with several males is a prerequisite for sperm competition, as it ensures the presence of sperm from more than one male in the female reproductive system (Simmons 2001). While multiple mating provides males with the advantage of producing more offspring, its prerequisites to females are less clear (Davies et al 2012), and numerous direct (genetic) and indirect (material) factors explaining its evolution have been proposed (Møller 1998; Simmons 2001; Davies et al. 2012).

Genetic benefits comprise the enhancement of progeny quality, which is achieved by the replacement of sperm from less desirable males by that of the favored individuals, and the possibility of broadening genetic variability of offspring. Indirect advantages include the gain of access to a wider range of natural resources, the avoidance of harassment or infanticide (Simmons 2001; Davies et al. 2012), or increased paternal care (Møller 1998). Females might also seek multiple partners in order to ensure fertility by gaining a greater volume of sperm (Simmons 2001; Davies et al. 2012). However, mating with more than one male is equally associated with numerous disadvantages, such as increased energetic and temporal costs or enhanced risks of sexually transmitted diseases and injuries sustained during copulation (Møller 1998).

Sperm competition is developed in numerous mammalian species, including several ungulates. The likelihood of its occurrence is elevated in species with long estrus duration, as well as in mating systems lacking female guarding by males and multimale groups. Contrarily, the evolution of sperm competition in monogamously living individuals is rather unlikely. The success of male's sperm is linked to its volume and the timing of mating in relation to ovulation (Clutton-Brock 2016). As a consequence, several morphological and behavioral adaptations in males evolved, potentially enhancing the likelihood of egg fertilization by the individual's sperm (Simmons 2001; Clutton-Brock 2016). Morphological changes include enlargement of testes, increased sperm production, and modification of sperm size, structure, or motility; while behavioral adaptations involve changes in the timing of breeding, repeated mating with the same female, and adjustment of ejaculated sperm count based on the intensity of sperm competition and the

probability of fertilization (Dixson & Anderson 2004; Clutton-Brock 2016). Nevertheless, Dixson and Anderson (2004) remarked that no evidence for the occurrence of sperm count modification was found in mammals.

Cryptic female choice is characterized as the internal and unobvious decision of females that determines which male becomes the father of their progeny (Birkhead 1998). As a result, the fact that an individual was chosen as a mating partner does not automatically imply that the female's offspring will be sired by this male (Eberhard 1996). Cryptic female choice can occur prior to fertilization (Birkhead 1998), as females discriminate against sperm of certain males and show preference for that of other males (Thornhill 1983). However, females might adopt choosy strategies after fertilization (Birkhead 1998), distributing nutrition unevenly among zygotes (Thornhill 1983). Numerous mechanisms of cryptic female choice have been proposed, including modifications of sperm transport and usage, ovulation, female reproductive tract morphology, reduction of investment into unborn offspring, or abortion (Eberhard 1996).

Sperm competition has been observed in Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*), where it is linked to the unusually high rates of copulations ewes engage in. Due to the relatively long duration of estrus, tending males are likely to be replaced by a more dominant individual while the female is still receptive. In addition to that, forced copulations gained by subordinate males via coursing strategies may occur. The dominant male also tends to remate with the female, once the subordinate individual retreats after a successful breeding. Consensual and forced copulations combined, an ewe can mate up to sixty times during a receptive period of two days, which presumably leads to sperm competition (Hogg 1988).

2.3.9. Sexual Selection and Sexual Dimorphism

Sexual selection is traditionally viewed as the principal cause for the development of sexual dimorphism (Ralls 1977), which is defined as a variation in secondary sexual characteristics, including body size and shape, coloring, ornaments, weapons, smell, or behavioral aspects, between males and females (Jarman 1983). However, according to Ralls (1977), the term "sexual dimorphism" often refers solely to the difference in body size, which is the most commonly observed type of dimorphism in mammals.

In the majority of mammalian species, males possess larger bodies in comparison to females (Anderson 1994). Bigger males are more likely to succeed in competitions for mating opportunities, which results in them being favored by sexual selection (Anderson 1994; Loison et al. 1999) and in the consequent development of size dimorphism between males and females (Loison et al. 1999). Anderson (1994) further proposed that larger bodies may enable males to force copulations and enhance sperm competition. Moreover, females might show a preference for males which are greater in size. Larger bodies presumably extend the time period during which males are capable of fighting for females, thus providing them with an advantage in endurance rivalry (Anderson 1994).

However, sexual selection cannot serve as the singular explanation for the development of sexual dimorphism (Ralls 1977; Anderson 1994; Loison et al. 1999). The character of mating systems has also been recognized as a factor influencing sexual dimorphism, with polygynous species generally displaying greater variability in size between males and females in comparison to monogamous species, which tend to be monomorphic (Ralls 1997; Anderson 1994; Weckerly 1998). Sexual dimorphism is equally related to ecological factors (Loison et al. 1999), as well as the size of the species, with a greater degree of sexual dimorphism being observed in larger species, compared to smaller ones (Anderson 1994; Loison et al. 1999).

2.4. Parentage and Paternity Assignment

Fitness is most frequently defined as the genetic contribution of an individual to the following generation (Vanpé 2007; Orr 2009), resulting from their capacity of survival and reproduction in the surrounding environment (Orr 2009). Emlen and Oring (1977) created an association between fitness and reproductive success, characterizing fitness as the measure of reproductive success of an individual in relation to the success of others. Orr (2009) identified viability, mating success, and fecundity as the principal fitness components causing the variance of offspring number among different individuals.

The fitness of males is primarily dependent on their ability to come victorious out of the competition for mates (Andersson 1994), which suggests the importance of their fighting capacities, as well as their significant body size and weapon development (Clutton-Brock

1985). Data on male reproductive success are relatively scarce and difficult to obtain in comparison to the information available on female success (Trivers 1972; Mooring & Penedo 2014), as the observed mating behavior of males does not necessarily correspond to the offspring sired by them (Coltman et al. 1999; Mooring & Penedo 2014; Clutton-Brock 2016).

In a study conducted by Mooring and Penedo (2014), a correlation between mating and reproductive success from a population perspective was found in male American bison (*Bison bison*), however, observed copulations only served as a poor indicator of individual reproductive success and paternity. Coltman et al. (1999) came to a similar conclusion in Soay sheep (*Ovis aries*), claiming the probability of seeing the sire greater if more consorts were observed, although the number of females a male accompanied could not ensure the correct estimation of his reproductive success.

Mooring and Penedo (2014) found that only 44% of the detected mating events in American bison resulted in the siring of offspring, and 60% of those failed to accurately predict the father. The authors identified mating with multiple males during one season, inability of males to fertilize, spontaneous abortion, and sperm competition as potential explanations, highlighting the improbability of the latter due to the fact that females only mate with one bull during each estrus (Mooring & Penedo 2014). Contrarily, the significance of sperm competition seems to be higher in Soay sheep (Coltman et al. 1999). Despite the favorable conditions, 60% of copulations in American bison remained unperceived, suggesting that alternative mating strategies, which are less likely to be observed than dominant tactics, may be adopted by males (Mooring & Penedo 2014). This finding is supported by Coltman et al. (1999), who stated that juvenile Soay rams and yearlings commonly use opportunistic or following mating strategies, and they are therefore rarely seen in consort with females whose offspring they sire, in contrast with adult males.

Contrarily, minimal difference was observed between behavioral and genetic measures of male reproductive success in a population of fallow deer (*Dama dama*). In only 16% of cases where both parents were known, and solely one male was seen to copulate with the female, was the sire assigned incorrectly. This was attributed to the rarity of the cases

where females mate with multiple males, as well as the ability to observe a large proportion of copulations (Say et al. 2003). Pemberton et al. (1992) saw an agreement of reproduction success measured by behavioral and genetic factors in a population of red deer (*Cervus elaphus*), which was associated with the fact that females only mate once and do not move between harems, making observation relatively uncomplicated. Nevertheless, the authors of both studies argued that paternity assignment based solely on behavioral estimates is unlikely to be accurate in species where females are highly mobile (Pemberton et al. 1992) and engage in copulations with multiple males (Pemberton et al. 1992; Say et al. 2003), or where males adopt alternative mating strategies (Say et al. 2003). In such cases where behavioral and genealogical relationships differ, accurate paternity assignment can solely be obtained by genetic methods (Coltman et al. 1999).

Microsatellites, also known as short tandem repeats or simple sequence repeats (Ellegren 2004; Oliveira et al. 2006), are the most commonly used markers in paternity assignment analyses (Städele & Vigilant 2016; Flanagan & Jones 2019). They are characterized as stretches of deoxyribonucleic acid (DNA) consisting of repeated mono-, di-, tri-, tetra-, penta-, or hexanucleotide units (Tóth et al. 2000; Ellegren 2004; Davies et al. 2012), which differentiates them from repeats of longer units called minisatellites or satellite DNA (Ellegren 2004). Microsatellites are located throughout the entire genome and can be found in parts coding proteins, as well as the non-coding regions (Tóth et al. 2000). They are immensely frequent in eukaryotic genomes, with their density being especially high in mammalian genomes (Ellegren 2004).

Parentage analysis using microsatellite markers is based on the principle of Mendelian inheritance (Flanagan & Jones 2019), where each individual possesses one allele of maternal origin and one allele of paternal origin (Städele & Vigilant 2016; Flanagan & Jones 2019). One of the principal advantages of microsatellites is their polymorphism (Ellegren 2004; Städele & Vigilant 2016; Flanagan & Jones 2019), with a multitude of allele variants possibly present at the loci (Oliveira et al. 2006; Flanagan & Jones 2019). Microsatellite variability is caused by the differences in their length (Ellegren 2004), resulting in homozygous individuals having two alleles with an identical number of repeats at the microsatellite locus, while each of the homologous chromosomes contains

a different number of repeats in heterozygous individuals (Oliveira et al. 2006). Despite having numerous perquisites, microsatellites are associated with certain disadvantages, the most prominent being their species-specificity and the consequent necessity of the development of new microsatellite markers for the majority of species (Abdelkrim et al. 2009). Such process includes locus identification, primer development, and polymerase chain reaction (PCR) optimization, which requires a significant temporal and financial investment (Abdelkrim et al. 2009; Flanagan & Jones 2019).

2.5. Social Structure and Mating in Elands

Elands are gregarious animals that typically form larger herds than other species of the *Tragelaphini* tribe (Hillman 1987; Wronski et al. 2006). Estes (1974) identified nursery herds, bachelor herds, and solitary adult males as three types of social arrangement found in common elands. Nursery herds are the largest aggregations of individuals, and they contain the greatest proportion of the population (Hillman 1987). They primarily consist of females and their calves, nevertheless, yearlings and subadults are equally present in these arrangements (Underwood 1975; Hillman 1987). Nursery herds are only joined by males after the peak of calving season (Underwood 1975), which Hillman (1987) explained by the postpartum character of estrus. Juvenile males leave the nursery herds and may subsequently accumulate in bachelor herds, which provide them with security until maturity is reached. Adult males are generally solitary (Estes 1974; Castelló 2016) and rarely engage with other individuals outside of the mating season (Estes 1974; Underwood 1975).

In Derby elands, females, juveniles, and calves are almost exclusively found in large herds, whereas males may adopt a solitary lifestyle or join smaller aggregations (Bro-Jørgensen 1997). Nonetheless, in a study conducted by Brandlová et al. (2018), groups containing individuals of both sexes were the most commonly observed social arrangements, implying that males equally tend to join herds, rather than wander alone. Bro-Jørgensen (1997) distinguished “file indienne” formation, tight formation, loose formation, and resting formation as four types of herd arrangement. “File indienne” formation, a long line of animals with calves accumulated in a crèche at the tail and males commonly found at the sides or behind the herd, is adopted during travel, movement in

dense habitats, and flight from predators. Tight formation is characterized by small distances among individuals with calves accumulated in a crèche, and it is established when elands are anxious or fleeing rapidly from a predator. Greater inter-individual distance, less order, and diminished tendency of calves to create crèches is typical for loose formations, adopted by elands while foraging. In resting formations, individuals are distributed more casually, however, calves are found in crèches (Bro-Jørgensen 1997).

Elands differ from the majority of other antelope species due to the absence of territoriality (Estes 1974; Owen-Smith 1977; Gosling 1986; Hillman 1987; Castelló 2016) and the existence of dominance hierarchy (Estes 1974; Leuthold 1974; Underwood 1975; Cransac & Aulagnier 1996; Wirtu et al. 2004; Castelló 2016). Underwood (1975, 1979) created an association between the two characteristics, stating that male elands are possibly dependent on dominance ranks to ensure access to females, since they cannot rely on territoriality. The gregariousness of elands also leads to the necessity of hierarchy establishment, as resources are exploited by a large number of individuals (Underwood 1975). Furthermore, the existence of dominance ranks diminishes the competition for resources, thus preventing elands from sustaining injuries (Kiley-Worthington 1978).

In a study of common elands conducted by Cransac and Aulagnier (1996), the dominant male was found to be superior to any females present in the herd, which led to both sexes being studied separately. Similarly, Kiley-Worthington (1978) stated that the oldest male acquired the highest position in the hierarchy, when judged by the frequency of threatening behavior adopted by elands. However, males did not consistently display higher ranks than females when the incidence of withdrawal, defined as a situation where an individual moved away when approached by another animal, was considered (Kiley-Worthington 1978). Cransac and Aulagnier (1996) remarked that dominance ranks were positively correlated with age in both male and female common elands, however, the authors concluded that the evolution of hierarchy cannot entirely be explained by this factor. Calves are not involved in the dominance hierarchy (Cransac & Aulagnier 1996), and juvenile individuals commonly occupy lower ranks in comparison to adults due to their less frequent engagement in threatening behavior (Kiley-Worthington 1978).

Physical characteristics have equally been recognized as factors affecting hierarchy in common elands (Cransac & Aulagnier 1996). Nevertheless, Wirtu et al. (2004) found a lack of correlation between body weight and dominance rank, remarking that neither was the most dominant female the heaviest, nor was the most subordinate one of the lightest weight. This implied that other factors are possibly more important in dominance rank determination (Wirtu et al. 2004). Maternal influence on the social rank of her young has also been proposed as a factor affecting hierarchy in common elands (Kiley-Worthington 1978; Cransac & Aulagnier 1996).

The hierarchy of common elands is traditionally described as unstable (Kiley-Worthington 1978; Wirtu et al. 2004), however, Underwood (1979) regarded the relationships among females as rigid. Common elands are characterized by low incidence of aggressive behavior (Kiley-Worthington 1978; Wirtu et al. 2004; Castelló 2016), with the interactions concerning hierarchy being essentially peaceful, consisting of the dominant individual approaching the subordinate one, who refrains from reacting (Underwood 1975) or deserts the area (Wirtu et al. 2004). Direct conflicts, where dominance rank of the superior individual is challenged, are scarce (Underwood 1975).

In a study of wild Eastern Derby elands, Bro-Jørgensen (1997) found that adult males and females are equal in terms of dominance determined by the occurrence of threatening behavior, which was attributed to the fact that females use threats to ward off unwanted sexual advances. Such hierarchy arrangement differs from that of captive Derby eland populations, where males possess higher ranks than females. Juveniles are subordinate to adult individuals of both sexes, and calves attain the lowest positions in the hierarchy (Bro-Jørgensen 1997). In a study conducted on a semi-captive population of Western Derby elands by Jůnková Vymyslická et al. (2015), the influence of sex on social ranking was not observed, which was attributed to the presence of horns in both males and females.

Age was found to be determinative only in the case of young growing individuals, whereas its importance was significantly diminished in mature adults. Social rank of females was equally observed to influence the rank of their progeny, however, it was unclear whether the offspring of dominant females possessed high social ranks due to

nepotism, heredity of determinative physical traits, the ability of dominant females to enhance body and horn growth of their young by ensuring access to resources, or other factors. Furthermore, the capacity of holding resources, shaped by body mass, body condition, and horn size, was also mentioned as a potential factor influencing hierarchy in adult Derby elands (Jůnková Vymyslická et al. 2015).

Jůnková Vymyslická et al. (2015) stated that changes in dominance ranks were relatively infrequent, and they primarily mirrored the capacity of Derby elands to hold resources, rather than their age. According to Bro-Jørgensen (1997), interactions within herds of Derby elands are predominantly peaceful, which may be attributed to the existence of dominance hierarchy. This finding is supported by Jůnková Vymyslická et al. (2015), who stated that the animals seemed to be aware of their position in the hierarchy and did not display tendencies to challenge elands of higher social ranks.

Male common elands occupy relatively small home ranges in comparison to females, which is beneficial to them since the number of potential competitors for mates is thus limited. Following strategies are adopted by males, consisting of pursuing various female groups as they enter the home ranges of males, rather than concentrating on following one female herd for a prolonged time period (Gosling 1986). The establishment of tending bonds and harems was equally observed in common elands (Underwood 1975).

Bro-Jørgensen (1997) observed smaller home ranges of Derby elands during the dry season in comparison to their total size. However, Švejcarová (2017) stated that home ranges are larger during the dry season, which may be attributed to the occurrence of rut or the scarcity of food sources during the dry season. Bro-Jørgensen (1997) suggested that the home ranges of solitary males are smaller in comparison to those occupied by nursery herds.

Sexual maturity in common eland is attained at 15-36 months of age (Castelló 2016) in females and at 18 months of age in males (Mungall 2007). Female common elands birth one offspring after a gestation period of 270-280 days (Castelló 2016). Underwood (1975) observed the majority of births between August and October. Parental care is predominantly provided by females (Underwood 1979; Gosling 1986; Bro-Jørgensen

2011), with the male investment being limited to the production of gametes. A strong mother-offspring bond is created (Gosling 1986), and females generally restrict their maternal behavior solely to their calf (Underwood 1975). Common elands are weaned at the age of six months (Castelló 2016), however, their bond with their mothers may persist for several years (Gosling 1986).

Female Western Derby elands reach sexual maturity at the age of 15-36 months, whereas males become sexually mature at 2-3 years of age (Castelló 2016). Bro-Jørgensen (1997) stated that wild female Eastern Derby elands are unlikely to be fertilized prior to attaining 25 months of age. In a study of semi-captive Western Derby elands conducted by Antonínová et al. (2008c), the average age of females at the time of conception was 24.56 months, however, the youngest individual was only 16.2 months old when fertilized. Bro-Jørgensen (1997) observed synchronous breeding in Eastern Derby elands, with the main rut occurring from December to February and the majority of births taking place between September and November. Similarly, in a study conducted by Koláčková et al. (2011a), mating of Western Derby elands was found to be synchronous, nevertheless, the majority of conceptions took place at the beginning of March, and 61% of calves were born in December.

Gestation in Derby eland lasts for 265 days and females traditionally birth one calf (Castelló 2016). Females leave their herds in order to give birth to their offspring (Antonínová et al. 2008a; Brandlová et al. 2018), and calves remain hidden from other herd members for approximately two weeks. During this period, females typically visit their progeny only in the morning and late afternoon, while rejoining the herd during the day. Calves are introduced to the herd at the age of two weeks, spending gradually prolonged time periods with the group, before joining it completely at the age of 15-20 days (Antonínová et al. 2008a). Bro-Jørgensen (1997) stated that calves were first seen to be moving with the herd at the age of two weeks. Upon joining the herd, a strong bond is established among young individuals, who accumulate in crèches, rather than spend time with their mothers (Bro-Jørgensen 1997; Antonínová et al. 2008a). Calves are weaned at the age of six months (Castelló 2016), and their mutual affection seems to wear off when the age of one year is reached. Juvenile individuals are freely dispersed among adult members of the herd from the age of 1.5 years (Bro-Jørgensen 1997).

2.5.1. Semi-captive Western Derby elands in Senegal

The unfavorable situation of Western Derby elands and the necessity for the implementation of protective measures to preserve the subspecies resulted in the establishment of a semi-captive population in the Bandia Reserve in 2000. Nine individuals, specifically five adult females, three subadult females, and one subadult male, were captured in the Niokolo Koba National Park and transported to the Bandia Reserve. However, three adult females died while placed in quarantine after the transfer (Antonínová et al. 2008b), failing to adapt to the change of conditions (Nežerková et al. 2004). The first semi-captive reproductive herd, Bandia 1, was thus initially composed of three adult females, two subadult females, and one subadult male (Antonínová et al. 2008b).

In 2006, the founder herd was divided into two breeding herds, which resulted in the creation of the Bandia 2 herd, originally including one male and three females. Furthermore, a bachelor herd of nine juvenile males was separated from Bandia 1 and transported to the Fathala Wildlife Reserve, creating the Fathala 1 herd. A third reproductive herd, Fathala 2, was established in 2008, containing one male from Fathala 1 and five females from Bandia 1 (Antonínová et al. 2008b). In 2009, the fourth breeding herd, Bandia 3, was created using one male and five females from Bandia 1 (Koláčková et al. 2009). Another reproductive herd, Fathala 3, was formed in 2011, containing one male and three females (Koláčková et al. 2011b). In 2012, a bachelor herd of seventeen males, Bandia 4, was established (Koláčková et al. 2012). Several fences in the Bandia Reserve were removed, causing the merge of the Bandia 1 and Bandia 2 herds. In addition to that, the enclosure where the Fathala 3 herd had been located was used for different purposes, and all individuals from this herd were thus introduced to the Fathala 2 herd (Brandlová et al. 2013). In 2014, the Bandia 5 breeding herd was established, originally containing one male and seven females (Brandlová et al. 2014).

In June 2019, the Bandia Reserve was inhabited by 77 Western Derby elands, 42 of which were males and 35 females. They were distributed among one bachelor herd, Bandia 4, and three reproductive herds, Bandia 1+2, Bandia 3, and Bandia 5. The Fathala Wildlife Reserve contained 38 Western Derby elands, precisely 19 males, 17 females, and two

animals of undetermined sex. These individuals were found in two breeding herds, Fathala 1 and Fathala 2 (Brandlová et al. 2020).

The semi-captive population of Western Derby elands in Senegal was established using fewer individuals than recommended for the population to be viable and have a satisfactorily large gene pool (Brandlová et al. 2020). In addition to that, only one founder male was used, which resulted in the elevated risk of inbreeding (Nežerková et al. 2004), with consequent decrease of heterozygosity and emergence of inbreeding depression (Zemanová et al. 2015). According to Brandlová et al. (2020), the reproduction herds in the Fathala Wildlife Reserve suffer from a diminished genetic quality in comparison to those in the Bandia Reserve, which emphasizes the necessity for a transfer of individuals between the reserves. The overall genetic diversity of the semi-captive Western Derby eland population represents 81.7% of the original genetic diversity, and it is expected to drop to 73.7% in the following 100 years, resulting in a decrease of viability and adaptability to changing conditions. An addition of at least six wild-captured animals would be required for the genetic diversity to maintain its current value (Brandlová et al. 2020).

The identity of each individual is determined based on the unique pattern of stripes on their body, which remains unchanged throughout life. Photographic documentation of nursing bouts is used to identify the relationships between mothers and calves. Until 2009, the only adult male was assumed to be the sire of all the young in the Bandia 1 reproduction herd. However, multiple males have been present in the breeding herds since 2010, increasing the difficulty of paternity assignment. Calves are thus recorded as multiple sired, with probability values assigned to each potential father. The number of such calves is constantly augmenting, since several planned translocations were impossible to accomplish (Brandlová et al. 2020). The knowledge of relationships between ancestors and offspring is necessary for the population management (Nežerková et al. 2004). Accurate pedigree analyses serve as an important tool in the management of Western Derby eland populations, and the completion and verification of the pedigree information via genetic methods is desirable (Koláčková et al. 2011a). Kubátová et al. (2020) concluded that in spite of the fact that Western Derby elands possess low genetic

polymorphism and high level of relatedness, a low degree of inbreeding is successfully maintained due to genetic management.

2.5.2. Captive common elands at the University Farm Estate Lány

The preparation for breeding of common elands in captivity by the Institute of Tropical and Subtropical Agriculture (ITSA), nowadays known as the Faculty of Tropical AgriSciences, Czech University of Life Sciences Prague (FTA CZU), was started in 1998. The principal aim of the establishment of a captive common eland population was to provide experts working on the conservation of Western Derby elands in Senegal with an experimental site to obtain information on breeding strategies in captivity (Kotrba 2004). The first five individuals, born in ZOO Dvůr Králové (FTA CZU 2018), were purchased in 2000 from the private farm Bio-Top Šidlov. Due to the lack of suitable premises owned by ITSA, the elands remained at the farm until 2002, when it ceased to exist, and the animals were consequently transferred to a private farm in Březová (Kotrba 2004). The elands have been kept at the University Farm Estate Lány under the management of FTA CZU since 2006 (FTA CZU 2018). Over the course of the years, the population has been enriched by the import of additional 38 animals from ZOO Dvůr Králové, six individuals from ZOO Ostrava, and three common elands originating from zoological gardens in Osnabrück, Germany; Mechelen, Belgium; and Borås, Sweden (Neradilová 2021, pers. comm.).

In January 2021, the total of fifty-six common elands was present at the University Farm Estate Lány, seventeen of which were males and thirty-nine were females. Sixteen individuals, specifically nine males and seven females, were born in 2020. The elands are distinguished based on the colorful ear tags, which are applied in the left ear of females and the right ear of males. Furthermore, each individual has a digital chip implanted, which equally facilitates their identification. During the monthly handling of the animals, body condition score and behavior is assessed, horn measurements are taken, and blood and fecal samples are collected. Several individuals are selected to be slaughtered each year in order to reduce the number of animals, and their meat is subjected to quality evaluation (Neradilová 2021, pers. comm.).

The structural organization of the facility allows the segregation of elands into smaller groups, however, no permanent arrangement is established, and the partition is done according to current requirements for the handling of animals. Parentage is principally assigned based on the observations of the eland keeper Petr Beluš, with the determination of maternity being relatively uncomplicated if births are seen. However, in the cases where births occur unperceived, the identity of the mother frequently remains unknown, as calves are aggregated in groups that are difficult to approach due to being guarded by one or several females, who are not necessarily the mothers of the calves. An effort to breed females exclusively between two and twelve years of age is made, however, the segregation of females outside this age range from males is not always possible, owing to the structure of the facility. Paternity is commonly impossible to determine since multiple potential sires are present in the herd. Genetic analyses therefore serve as the sole method of parentage assignment in common elands kept at the University Farm Estate Lány (Neradilová 2021, pers. comm.).

3. Aims of the Thesis

The first aim of the thesis was to perform paternity assignment in Western Derby elands in the Senegalese semi-captive populations in the cases where paternity was unclear and to compare the obtained results with the predictions based on body condition and observations, which are recorded in the annually published studbooks. The second aim was to determine parentage in the captive population of common elands kept at the University Farm Estate Lány and to clarify parentage relations among the individuals.

Hypotheses:

- I.) The results of paternity assignment in the Western Derby elands will correspond to the predictions, with large males in the best condition siring the majority of offspring.

- II.) Paternity determination in the common elands using molecular methods will mirror the predictions based on observations.

4. Methods

4.1. Western Derby Elands

In the case of Western Derby elands, molecular data had already been gathered and edited by Kubátová et al. (2020), therefore no laboratory work was required. For each individual with an unknown father, the paternity of all putative sires proposed in the Western Derby eland studbook (Brandlová et al. 2020) was tested by the comparison of their genotypes to those of their potential offspring. Maternal genotypes were equally taken into consideration, since mothers were known in the majority of cases. If a mismatch among the genotypes was detected, paternity was rejected. In order to assess the relation between body condition and paternity, the results were compared with the probabilities of siring the offspring attributed to the males based on their physical state, which were provided by Brandlová (2021, pers. comm.).

4.2. Common Elands

Blood, tissue, or hair samples were obtained from elands kept at the University Farm Estate Lány during regular handling of the animals. DNA extraction, polymerase chain reaction, and preparation of reaction mixture for fragmentation analysis were carried out in the Laboratory of Molecular Genetics at FTA CZU.

4.2.1. DNA Extraction

Genomic DNA was extracted from the samples using QIAmp DNA Blood Mini Kit (Qiagen) for blood samples and DNeasy Blood & Tissue Kit (Qiagen) for tissue and hair samples, following the steps listed in the enclosed protocols. Concentration of the extracted genomic DNA was measured with the NanoDrop One UV-Vis Spectrophotometer (Thermo Fisher Scientific).

4.2.2. Polymerase Chain Reaction (PCR)

Polymerase chain reaction was performed in the T100 Thermal Cycler (BIO-RAD) in 10 µl of the reaction mixture, containing 5 µl of Multiplex PCR Master Mix, 3 µl of RNase-Free Water, 1 µl of primer mix, and 1 µl of genomic DNA. The Multiplex PCR

Master Mix and the RNase-Free Water were taken from the QIAGEN Multiplex PCR Plus Kit (Qiagen). The PCR protocol is given in Table 1. Two polymerase chain reactions were carried out for every sample, with a different primer mix used each time. The composition of the two primer mixes, labeled E1 and E2, is listed in Tables 2.

Table 1: Polymerase chain reaction protocol

step	temperature (°C)	duration (min)
1	95	5:00
2	95	0:30
3	60	1:30
4	72	0:30
5	go to step 2, 35×	
6	68	30:00
7	12	forever

Table 2: Composition of primer mixes E1 and E2

	marker	fluorescent dye	size range (bp)
E1	BL42	FAM	278-320
	BRR	NED	230-268
	ETH10	FAM	198-234
	SPS115	FAM	240-270
	SPS113	PET	122-155
	X80214	VIC	198-243
E2	BM4505	FAM	235-292
	CSSM42	PET	156-230
	CSRM60	FAM	79-129
	INRA107	FAM	140-190
	BM1818	VIC	248-276
	ETH225	NED	132-166

4.2.3. Fragmentation Analysis

The reaction mixture for fragmentation analysis consisted of 8.5 μ l of formamide, 0.5 μ l of GeneScan 500 LIZ dye Size Standard (Applied Biosystems), and 1 μ l of PCR product. The mixture was incubated in the T100 Thermal Cycler (BIO-RAD) for 5 minutes at 95°C, with the lid temperature set to 105°C. Fragmentation analysis was performed by the service laboratory of the Faculty of Science, Charles University.

4.2.4. Data Analysis

Data from the fragmentation analysis were edited using the Geneious 10.2.6. software (Geneious), and the genotypes of the individuals were reconstructed. Parentage was assessed based on observational predictions provided by Neradilová (2021, pers. comm.) by the comparison of genotypes of each individual with those of their putative parents. In the case of a disaccord among the genotypes, parentage was rejected.

5. Results

5.1. Western Derby Elands

Paternity was tested for all potential fathers of 41 individuals based on the predictions recorded in the Western Derby eland studbook (Brandlová et al. 2020) using twelve microsatellite markers. The paternity of all putative fathers but one was rejected in eighteen instances, leaving each of these individuals with only one possible sire. In another nineteen cases, the number of potential fathers was narrowed down, however, multiple males remained as probable sires. No elimination was possible in three cases and both potential fathers were eliminated in one instance. In the latter case, Dering (ID 1030) was identified as the sire of Salma (ID 1149), despite not being mentioned among the potential fathers. The results of paternity assignment are presented in Appendix 2.

In the process of paternity determination, an inaccuracy in maternity assignment was found in the case of Bouba (ID 1132). The proposed mother Bunta (ID 1095) was therefore rejected, and Guddi (ID 1011), who had been mentioned as the mother of Bouba in several reports (Brandlová 2021, pers. comm.), was identified as Bouba's mother. Nevertheless, this finding did not have an impact on the paternity assignment, since no additional rejections of potential sires of Bouba could be made after the identification of the mother.

Furthermore, during the clarification of Guddi's maternity of Bouba, a supplementary discord in paternity assignment was found in the case of Georgina (ID 1035), who was supposed to have been sired by Niokolo (ID 1001). Since this male had been the sole proposed potential father, paternity was not initially tested in this instance and was only verified when the mismatch was found. Karang (ID 1010) was identified as the sire of Georgina, which had not been expected due to his young age, being only three years and one month old at the time of Georgina's birth.

Overall, the results correspond to the predictions based on physical condition provided by Brandlová 2021 (pers. comm.), with the paternity of individuals in a supreme physical state rarely being denied. Out of the 28 instances where solely one male had been

identified as the most probable sire, only in the case of Duggi (ID 1052) was this male rejected as a potential father. In the four cases where multiple males had been proposed as the most plausible putative fathers, paternity assignment never eliminated all of them. In the remaining nine instances, all proposed sires had been attributed the same probability of being the father. These results are presented in Appendix 2.

5.2. Common Elands

Paternity determination using twelve microsatellite markers was performed in eight sampled animals born in April 2018 and sixteen sampled individuals born in February and March 2019, whose sires had not been identified in reports from the regular handlings. Three males of appropriate age at the time of conception were taken into consideration due to their reproductive success in other time periods. Dael (no ear tag) and Hanno (no ear tag) had been identified as the sires of the individuals born between July 2014 and August 2017. Drak (ET 181) had been reported as a father of the calves born after November 2019. While the paternity of Drak was rejected in all twenty-four instances, no conclusions regarding Dael and Hanno could initially be made, as these individuals had not been sampled.

Since Dael had been indicated as the father of sixteen sampled animals born prior to 2018, his genotype could be partially reconstructed based on the genotypes of these individuals and their mothers. Two of these animals, ET 218 and ET 224, did not match the remaining fourteen individuals, indicating that they had been sired by a different male. In the instance of ET 224, Drak was identified as the potential father, having already been three years and six months old at the time of the birth of ET 224. On the contrary, the father of ET 218 was impossible to identify.

A similar approach was attempted in the case of Hanno, who had been identified as the father of eight sampled animals born prior to 2018. However, his genotype could not be reconstructed since the genotypes of his proposed offspring indicate that they had not been sired by the same male. The genotypes of three of these animals, ET 207, ET 208, and ET 209, correspond to the reconstructed genotype of Dael, therefore suggesting that he may have been their sire. Nevertheless, the paternity of Dael was rejected in the other

five animals, and the genotypes imply that these individuals had been fathered by the minimum of two males, whose identity remains unknown.

While the reconstructed genotype of Dael agrees with the genotypes of all sixteen individuals born in February and March 2019, it corresponds to solely three individuals born in April 2018, with paternity of this male being rejected in the remaining five calves born in April 2018. The genetic makeup of four of these animals, ET 227, ET 228, ET 229, and ET 231, suggests that they may have been sired by one male, nevertheless, his genotype does not match that of the remaining individual, ET 232. While ET 232 may share a father with one or more of the six individuals born prior to 2018 whose sires were impossible to identify, the potential father of ET 227, ET 228, ET 229, and ET 231 could not have sired any of the six individuals with unknown fathers born prior to 2018.

These results suggest that at least three unidentified males contributed to the reproduction in 2017 and 2018. Three older males, Hanno, Camel (ET 143), and ET 117, born in July 2007, May 2011, and November 2011, respectively, were present in the herd during that time period. In addition to that, the herd contained more than ten younger males, who were of age suitable for reproduction in 2017 or 2018 and may have thus sired some of the offspring. Nevertheless, none of these males had been sampled, therefore no further identification is possible. The detailed results of paternity determination are presented in Appendix 3.

In addition to paternity assignment, maternity was tested for the putative mothers of thirty-three individuals born prior to 2020, with a rejection being made in five out of the twenty-nine calves who had been attributed with one potential mother each. Since three of these young had been supposedly sired by Viktoria (ET 63) and two by Toulavka (ET 58), the accuracy of ear tagging was questioned. A sample labeled with Toulavka's microchip number, which had not been taken from the individual with the ear tag 58, was later found, therefore implying that the ear tag 58 had been applied to the incorrect eland. The sample 58 was attributed to Cavalia (ET 66) based on the comparison of the genotype obtained from this sample and those of Cavalia's offspring, and Toulavka was further regarded as unsampled, since the sample marked with the microchip number is yet to be

processed. As no conclusion could be made about Viktoria and the sample 63 had been labeled with a question mark, this individual was equally considered as unsampled.

In two of the remaining instances, Berta (ET 188) had been identified as the mother of ET 250 and ET 251 in different reports, however, she could not have birthed both of them, since they were born two days apart. After the comparison of the genotypes, maternity of Berta was rejected for ET 250 and confirmed for ET 251. In the last two cases, Lorie (ET 61) and ET 167 had been identified as the mothers of ET 258 and ET 259 in written records, nevertheless, it had been unclear which of these females gave birth to which offspring. Maternity of Lorie was confirmed for ET 259, and ET 167 was determined as the mother of ET 258.

Parentage assignment was also performed for all twenty-one calves born in 2020. Paternity of Drak, the only male of suitable age present in the herd at the time of conception, was verified and confirmed in all cases. The genotype comparison showed that out of all the females found in the herd throughout 2020, only twenty-one of them could have been the mothers of the calves. The only unsampled young individual born in 2020, ET 280, had been identified as the progeny of ET 167, and since this female could not be attributed to any other calf, this identification was regarded as accurate. Maternity assignment was successful in sixteen cases, with the remaining four individuals being assigned to four unsampled females. The results are summarized in Appendix 3.

6. Discussion

Parentage assignment in the Senegalese semi-captive populations of Western Derby elands and the captive population of common elands kept at the University Farm Estate Lány was performed using twelve microsatellite markers. In the case of Western Derby elands, one of the twelve loci, CSSM42, was monomorphic, however, this had been known prior to its usage and it had been included due to the design of the study (Štochlová 2016). No case of monomorphism was observed in the common eland loci. Out of the twelve microsatellite markers used in common elands, SPS113 and CSSM42 failed to amplify properly and therefore could not have been utilized for parentage determination. Although the origin of this issue is unknown, the fact that the selected microsatellite markers are not specific to elands may serve as a plausible explanation. Despite microsatellites being capable of cross-specific amplification (Oliveira et al. 2006), mutations may occur in different species and negatively impact the amplification process (Jarne & Lagoda 1996). In addition to that, the length ranges of microsatellites had to be modified due to their nonspecificity to elands.

Overall, the results of paternity assignment in Western Derby elands correspond to the hypothesis, with larger males in the best condition siring the majority of offspring. The same conclusion was reached in a study conducted by McElligott et al. (2001), where male mating success in fallow deer was found to be correlated with body size. Similarly, body dimensions were identified as an important factor determining reproductive success in white-tailed deer (Newbolt et al. 2017) and Soay sheep (Preston et al. 2003). In addition to that, male breeding success was found to be influenced by body mass in white-tailed deer (Jones et al. 2011), and indirect relatedness between the two values was observed in fallow deer, with the individuals' body weight affecting their dominance rank, which consecutively impacted their reproductive success (McElligott et al. 2001). No conclusion regarding the relation of body condition and paternity could be made in the common elands kept at the University Farm Estate Lány since the monitoring of this factor has started only recently.

While paternity relations determined using molecular methods generally agreed with the predictions in the Western Derby elands, mismatches were more frequent in common

elands, contrary to the hypothesis, which may have been caused by the nature of the populations. Since the management of the semi-captive populations of Western Derby elands significantly impacts the entire subspecies, the pressure put on the gathering of detailed and accurate information regarding the animals is higher than in the case of common elands kept at the University Farm Estate Lány. Paternity assignment in the common elands in Lány is encumbered by the fact that the segregation of the animals into groups is temporary and unrecorded. It is thus impossible to determine which males had had access to the mothers of the calves at the time of conception and could have therefore sired the young. In addition to that, Western Derby elands in the Bandia reserve and the Fathala Wildlife Reserve are primarily identified using the permanent and unique stripe pattern (Brandlová et al. 2020), whereas the identity of common elands at the University Farm Estate Lány is principally determined by the colorful ear tags, which are prone to falling off (Neradilová 2021, pers. comm.), making accurate identification of the individuals more difficult.

The results in Western Derby elands contrast with the studies conducted on Soay sheep by Coltman et al. (1999) and on American bison by Mooring and Penedo (2014), where a disparity between paternity assignment based on observations and paternity determinations using molecular methods was found. Contrarily, Say et al. (2003) regarded observations as relatively accurate predictors of parentage relations in fallow deer, however, genetic methods rejected paternity of the only male seen mating with the mother of the fawn in 16% of the cases. Nevertheless, these studies were performed on animal populations containing between 400 and 900 individuals, contrary to the herds studied in this thesis, which only consisted of several tens of elands. The contrasting results could be explained by this difference in population size, since the smaller number of potential sires in Western Derby elands likely facilitated the prediction of paternity and increased its accuracy.

A reproductive skew was observed in both Western Derby elands and common elands, with the majority of calves born in a certain time period being sired by one male and the involvement of other males in the reproduction being minimal or nonexistent. A similar uneven distribution of paternities with a large proportion of the offspring sired by a small group of males was found in several ungulate species, such as Soay sheep (Coltman et al.

1999), fallow deer (Say et al. 2003), reindeer (Røed et al. 2002), and Alpine ibex (Willisch et al. 2012).

The results of paternity determination in common elands kept at the University Farm Estate Lány suggest that Dael played a major role in the reproduction between 2014 and 2018, likely siring more offspring than he had been assigned based on observations. Contrarily, Hanno, who had been regarded as the second most successful male, could not have sired all the offspring he had been associated with in the written reports. A similar conclusion was reached by Mooring and Penedo (2014) in American bison, where behavioral observations underestimated the reproductive success of the males most involved in reproduction, while overestimating the number of offspring sired by less successful males. Nonetheless, this statement does not correspond to the remaining males who were must have contributed to the reproduction in common elands kept at the University Farm Estate Lány, since they had not been identified in any written reports as sires of the calves, and their reproductive success had thus been underestimated by behavioral observations.

The minimal reproductive contribution of Hanno could be attributed to the fact that Dael had been present in the herd for eleven months and had already sired a number of offspring at the time of Hanno's arrival. Markussen et al. (2019) observed a similar situation in adult male moose, where the annual reproductive success was positively influenced by the number of young fathered in the previous year. However, the mechanism which led to the occasional siring of offspring by males other than Dael remains unclear, since no data on the segregation of the herd into the two parts of the facility are available. Consequently, it cannot be determined whether the sires were achieved due to Dael being separated from these males, adoption of alternative mating strategies, successful confrontation of Dael, or other methods..

Since the access of males to mating partners is influenced by dominance status (Wirtu et al. 2004), and a positive correlation between dominance ranks, and male reproductive success was found in many ungulate species, including Alpine ibex (Willisch et al. 2012), fallow deer (McElligott et al. 2001; Say et al. 2003), mountain goats (Mainguy et al.

2008), reindeer (Røed et al. 2002), and American bison (Mooring & Penedo 2014), paternity analysis may provide an insight into the dominance hierarchy of elands.

The results imply that dominance ranks in the common eland herd kept at the University Farm Estate Lány are relatively stable, with Dael gaining the supreme position in the hierarchy after the death of Boris, who had been the primary sire of offspring conceived prior to Dael joining the herd, in August 2015 and retaining the status until his leaving the facility in September 2018, when he was replaced by Drak. This finding contrasts with the results obtained by Kiley-Worthington (1978) in a captive population of common elands, where an instability of male dominance ranks was observed. Furthermore, the fact that Hanno was one year and eight months older than Dael but failed to attain a higher social rank suggests that age is not necessarily an accurate determinant of dominance hierarchy within the herd. This conclusion is in accord with the results of a study conducted by Cransac and Aulagnier (1996), where social rank of common elands could not solely be explained by age, despite this factor having a significant impact on the dominance hierarchy.

Paternity assignment in Western Derby elands revealed a shift in the reproductive success of males over the course of time, with older males being gradually replaced by younger individuals in a better condition. This dome-shaped pattern of male reproductive success, with the number of offspring initially increasing with age, peaking in prime-aged individuals, and decreasing in senescence, is typical for many ungulate species (Vanpé et al. 2009). It has been observed in Alpine ibex (Willisch et al. 2012), bighorn sheep (Festa-Bianchet 2012), roe deer (Vanpé et al. 2009), and white-tailed deer (Sorin 2004). Furthermore, Mooring and Penedo (2014) found that the likelihood of mating not resulting in conception was higher in older American bison males. The male common elands kept at the University Farm Estate Lány are commonly slaughtered, sold, or die prior to reaching senescence. Since only eight males in the history of the captive population attained or surpassed the age of five years old, no conclusion regarding the change of reproductive success with age can be made.

In Western Derby elands, Georgina (ID 1035) was found to have been sired by Karang (ID 1010), who had only been three years and one month old at the time of Georgina's

birth. Siring of offspring by young males has been recorded in several other ungulate species, such as roe deer (Vanpé et al. 2009), white-tailed deer (Sorin 2004; Neuman et al. 2016), Alpine ibex (Willisch et al. 2012), and Soay sheep (Coltman et al. 1999). Karang's successful reproduction at such a young age could be explained by the fact that Georgina's mother Guddi (ID 1011) had been exceptionally young (Brandlová 2021, pers. comm.), equally being only three years and one month old at the time of Georgina's birth. In a study conducted by Sorin (2004) on white-tailed deer, yearling males were found to primarily mate with young females, presumably due to the inability to outcompete more dominant males and access older females. However, the findings of Neuman et al. (2016) contrast with these results, recording the cases of young white-tailed deer successfully mating with older females. Similarly, maternal age could not explain the potential paternity of Drak in the case of ET 224 in common elands at the University Farm Estate Lány, since the supposed mother Cavalia (ET 66) had already been over eight years old at the time of birth of ET 224.

Maternity assignment performed in the thirty-three common eland calves born at the University Farm Estate Lány prior to 2020 rejected the mother recorded in the written reports in only five instances. Since these five young had been associated with solely two females, this inaccuracy was likely caused by the difficult identification of these females or incorrect ear tagging. The remaining instance where the mother was impossible to determine was issued from the fact that one eland had originally been attributed to two calves who could not have been birthed by the same female, and no other potential mother had been proposed. In the case of common eland calves born in 2020, the mothers of eleven individuals had been identified in the written reports, and maternity was confirmed by molecular methods in all eleven instances. In the remaining nine sampled calves, where the mothers had either been referred to solely by physical traits or ear tag color, or no information had been provided, maternity was determined in five cases. These findings imply that in the majority of the cases where maternity assignment based on observations is feasible, the obtained results are accurate.

7. Conclusions

Paternity assignment via molecular methods was performed in forty-one Western Derby elands from the Senegalese semi-captive populations. Overall, the results corresponded to estimations based on body condition, with the majority of offspring being sired by males in a supreme physical state. Paternity relations were equally assessed in twenty-four captive common elands kept at the University Farm Estate Lány. Although paternity predictions were principally accurate in the cases where the most successful male had been identified as the sire in the written reports, molecular methods revealed that behavioral observations likely overestimated the reproductive success of the presumably second most successful male, and more individuals seem to have been involved in the reproduction than had previously been anticipated. Furthermore, maternity was determined in fifty-four common elands, and in most of the cases where putative mothers had been recorded in written reports, maternity of these females was confirmed.

The results of this thesis therefore suggest that male body condition generally serves as an accurate predictor of parentage relations in Western Derby elands in the Bandia Reserve and the Fathala Wildlife Reserve, and behavioral observations can correctly predict maternity in the common eland herd kept at the University Farm Estate Lány. However, the accuracy of paternity estimations based on observations in the common elands is diminished, and the instances where no observations can be made, visual identification of the individuals is impossible, or certain animals are unexpectedly involved in the reproduction, molecular methods serve as the sole reliable determinants of parentage relations.

However, these relations cannot be fully resolved if an insufficient number of samples is available. Consequently, acquisition of samples from the common eland males who had supposedly been involved in reproduction in the herd kept at the University Farm Estate Lány would be beneficial for further clarification of parentage relations among the individuals. Moreover, verification of the identity of the elands with ear tags 58 and 63 using ear notches and sampling of the remaining putative mothers of the calves born in 2020 is desirable since it might provide a deeper insight into maternity relations.

The information on paternity recorded in the annually published Western Derby eland studbook will be updated based on the findings from this thesis. Furthermore, the obtained results on parentage in the common eland herd at the University Farm Estate Lány will further be used for the management of the population.

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Appendices

List of the Appendices:

Appendix 1: Common eland samples

Appendix 2: Paternity assignment in Western Derby elands

Appendix 3: Parentage assignment in common elands

Appendix 1: Common eland samples

Table 3: List of sampled common elands

ear tag	ear tag color	name	sex	type of sample
36	blue	Lina	F	blood
41	green	Sydney	F	tissue
56	blue	Tora	F	blood
57	red	Eliška	F	blood
61	blue	Lorie	F	blood
66	red	Cavalía	F	blood
80	pink	Gimbia	F	tissue
81	blue	Lubumba	F	blood
84	green	Ghana	F	blood
132	red	-	F	blood
156	yellow	-	F	blood
158	orange	-	F	blood
164	yellow	-	F	blood
167	pink	-	F	blood
181	yellow	Drak	M	hair
188	pink	Berta	F	blood
194	orange	-	F	blood
195	pink	Ninvaze	M	tissue
198	yellow	-	M	blood
199	red	-	M	blood
200	green	-	F	blood
201	orange	-	F	blood
202	green	-	M	blood
203	orange	-	M	blood
204	red	-	F	blood
205	yellow	-	F	blood
206	yellow	-	M	blood
207	pink	-	F	blood
208	pink	-	M	blood
209	orange	-	M	blood
212	green	-	F	tissue
215	yellow	-	F	blood
218	pink-red	-	F	blood
219	pink	-	F	blood
221	yellow	-	M	tissue

Table 3: List of sampled common elands (continued)

ear tag	ear tag color	name	sex	type of sample
222	green	-	M	blood
223	pink	-	F	blood
224	yellow	-	F	blood
225	pink	-	M	Blood
226	yellow	-	M	Blood
227	pink	-	F	Blood
228	yellow	-	M	Blood
229	yellow	-	M	Blood
230	yellow	-	M	blood
231	pink	-	F	blood
232	yellow	-	M	blood
233	pink	-	F	blood
247	yellow	-	F	tissue
248	red	-	F	blood
249	orange	-	F	blood
250	pink	-	F	blood
251	pink	-	M	blood
252	red	-	F	blood
253	orange	-	F	blood
254	red	-	M	blood
255	pink	-	F	blood
256	green	-	F	blood
257	yellow	-	M	blood
258	yellow	-	M	blood
259	red	-	M	blood
260	pink	-	M	blood
261	orange and red	-	F	blood
262	red	-	F	blood
266	yellow	-	M	blood
267	pink	-	M	blood
268	yellow	-	F	blood
269	pink	-	M	blood
270	yellow	-	M	tissue
271	orange	-	F	blood
272	yellow	-	M	blood
273	pink	-	F	blood

Table 3: List of sampled common elands (continued)

ear tag	ear tag color	name	sex	type of sample
274	white	-	F	blood
275	yellow	-	M	blood
276	yellow	-	M	blood
277	white	-	F	blood
278	white	-	M	blood
279	red	-	F	blood
281	red	-	M	blood
282	green	-	M	blood
283	green	-	F	blood
284	blue	-	M	blood
285	blue	-	M	blood
286	blue	-	M	blood
287	red	-	F	blood

Appendix 2: Paternity assignment in Western Derby elands

Table 4 summarizes the results of paternity assignment performed in Western Derby elands. Identification numbers of the most probable sires of the individuals, identified based on physical condition by Brandlová (2021, pers. comm.), are marked in bold. If no identification number is marked, all of the proposed fathers had been attributed the same probability of being the sire.

Table 4: Results of paternity assignment in Western Derby elands

ID	potential sires	eliminated sires
1073	1001 1033	1037
1075	1001 1033	1037
1078	1001 1033	1037
1087	1001 1033	1037
1088	1001 1033	1037
1092	1001 1033	1037
1094	1001 1033	1037
1096	1033 1037	1001
1105	1033	1001 1037
1109	1017	1062
1110	1033	1001 1037
1115	1017	1062
1116	1017	1062
1117	1033	1001 1037
1118	1017 1062	-
1119	1017	1062
1120	1033 1037	1001
1122	1033 1037	1001
1126	1037 1059	1017 1062 1073
1128	1037	1017 1059 1062 1073
1132	1037 1059 1073	1017 1062
1133	1017 1062	1037 1059 1073

Table 4: Results of paternity assignment in Western Derby elands (continued)

ID	potential sires	eliminated sires
1137	1022	1010
1139	1059 1092	1062 1073 1084 1088 1089 1097 1102
1140	1059 1073	1062 1084 1088 1089 1092 1097 1102
1141	1059	1062 1073 1084 1088 1089 1092 1097 1102
1144	1059 1073	1062 1084 1088 1089 1092 1097 1102
1147	1059	1062 1073 1084 1088 1089 1092 1097 1102
1148	1059	1062 1073 1084 1088 1089 1092 1097 1102
1149	-	1094 1110
1150	1022 1104	-
1151	1022 1104	-
1152	1072	1101 1108
1153	1072	1101 1108
1154	1059 1062 1073 1084 1092	1088 1089 1097 1102 1109 1115
1157	1059	1062 1073 1084 1088 1089 1092 1097 1102 1109 1115
1158	1059 1073	1062 1084 1088 1089 1092 1097 1102 1109 1115
1159	1048	1022
1160	1048	1022
1163	1084 1088 1102	1059 1062 1073 1089 1092 1097 1109 1115
1165	1094	1110

Appendix 3: Parentage assignment in common elands

Table 5: Results of paternity assignment in common elands

animals born in April 2018		animals born in February and March 2019	
ET	sire	ET	sire
226	Dael (no ET)	247	Dael (no ET)
227	unknown	248	Dael (no ET)
228	unknown	249	Dael (no ET)
229	unknown	250	Dael (no ET)
230	Dael (no ET)	251	Dael (no ET)
231	unknown	252	Dael (no ET)
232	unknown	253	Dael (no ET)
233	Dael (no ET)	254	Dael (no ET)
		255	Dael (no ET)
		256	Dael (no ET)
		257	Dael (no ET)
		258	Dael (no ET)
		259	Dael (no ET)
		260	Dael (no ET)
		261	Dael (no ET)
		262	Dael (no ET)

Table 6: Results of maternity assignment in common elands

animals born prior to 2020		animals born in 2020	
ET	dam	ET	dam
158	unknown	267	ET 205
164	Lina (ET 36)	268	ET 204
194	unknown	269	Gimbia (ET 80)
198	Tora (ET 56)	270	ET 224
199	Eliška (ET 57)	271	ET 201
200	Lorie (ET 61)	272	ET 200
201	unknown	273	ET 218

Table 6: Results of maternity assignment in common elands (continued)

animals born prior to 2020		animals born in 2020	
ET	dam	ET	dam
202	Ghana (ET 84)	274	Eliška (ET 57)
203	unknown	275	Toulavka (ET 58) Viktoria (ET 63) Volta (ET 89) ET 211
206	Sydney (ET 41)	276	Berta (ET 188)
207	Lina (ET 36)	277	ET 194
215	ET 156	278	Toulavka (ET 58) Viktoria (ET 63) Volta (ET 89) ET 211
219	Eliška (ET 57)	279	Lubumba (ET 81)
221	Lorie (ET 61)	280	ET 167
222	Ghana (ET 84)	281	Cavalía (ET 66)
223	unknown	282	ET 156
225	ET 132	283	Toulavka (ET 58) Viktoria (ET 63) Volta (ET 89) ET 211
226	ET 167	284	ET 132
227	ET 164	285	Tora (ET 56)
228	Sydney (ET 41)	286	Lina (ET 36)
229	Lina (ET 36)	287	Toulavka (ET 58) Viktoria (ET 63) Volta (ET 89) ET 211
247	ET 164		
250	unknown		
251	Berta (ET 188)		
254	Tora (ET 56)		
255	Lina (ET 36)		
256	ET 156		
257	Eliška (ET 57)		
258	ET 167		
259	Lorie (ET 61)		
260	ET 194		
261	ET 158		
266	ET 194		