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Reproductive behaviour of eland (*Taurotragus oryx*)

Master's thesis

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Declaration:

I hereby declare that this thesis entitled Reproductive behaviour of common eland (*Taurotragus oryx*) is my own work and all the sources have been quoted and acknowledged by means of complete references.

In Říčany 25. 4. 2018

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Abstract:

Successful reproduction is one of the most crucial aspects of animal husbandry. The understanding of the behaviour during reproduction may prevent some aggressive encounters in group living animals and may increase the potential quality of next progeny or increase reproductive success in general, especially in non-domesticated species. As reproductive behaviour of common eland (*Taurotragus oryx*) is not studied in detail and quantified, I focused on farmed herd belonging to Czech University of Life Sciences in Lany (Czech Republic). I recorded a group of nine females and a male continuously for one month on cameras installed in the barn and analysed their behaviour prior, during and after the copulation. The aim was to find out if the length of copulation will be influenced by the male's behaviour towards the female prior to copulation (licking, rubbing etc.) or by the response of the female. I calculated the length of pregnancy as a time between mating and the calf delivery which was 273.53 ± 2.33 days (mean ± SD) and compared it with other studies. Results show that the length of copulation was 4.08 ± 0.63 s (mean ± SD) and was not influenced by the male's behaviour prior to the mating or by female's behaviour towards the male (wrestling etc.). Time between copulations was influenced by the behaviour of the female during the copulation, when the female froze the mean time between copulations was shorter in comparison when she ran away. But to understand reproductive behaviour better, more studies with different males need to be done to fully understand complexity of eland reproduction.

CONTENTS

LIST OF FIGURES

1. INTRODUCTION

Common eland (*Taurotragus oryx*) is together with the giant eland (*Taurotragus derbianus*) one of the largest African antelope (Pappas 2002). Thanks to its large body mass, high quality meat and milk production, social behaviour and calm nature it is referred to as an intermediate species between antelopes and bovids (Treus & Kravchenko 1968), therefore it is a good animal for experimentation and farming under domestication effort (Woodford 2000). However, management-wise, successful reproduction is a key factor to animal husbandry as the understanding of reproductive behaviour may help to prevent unnecessary aggression between animals or even increase the quality potential of progeny. The topic of reproductive behaviour of eland is still not satisfactory detailed and quantified, therefore more studies are needed.

Eland is well adaptive and there is a great potential for eland to adapt to conditions of Central Europe therefore eland was chosen by FAO as a species to domesticate (Scherf & Organization 2000). One of this experimental farms is located in the middle of Europe in Lány (Czech Republic) near Prague. It belongs to the Czech university of Life Sciences in Prague, Faculty of Tropical AgriSciences (former Institute of Tropics and Subtropics) under supervision of Radim Kotrba, PhD. Elands are bred there since 2006, formerly the group was consisted of 5 animals (all of them were born in the Zoo Dvůr Králové nad Labem), nowadays there are about 50 animals. The main objective of this farm is to evaluate the potential of eland as an alternative species bred in conditions of Central Europe, as well as experimental field for students of ČZU doing their master's thesis and dissertation. The most important role of this farm is a research of this still quite unexplored species (Zejdová 2009).

2. LITERATURE REVIEW

2.1. MATING STRATEGIES OF UNGULATES

In mammals, males show various types of mating bonds like obligate monogamy, group polygyny and promiscuity. They are associated with a variety of different forms of mate guarding, including the defence of feeding and mating territories, the defence of female groups and the defence of individual receptive females. Compared to birds, where over 90 % of species were believed to be mostly monogamous, more than 90 % of mammalian species' males are habitually polygynous (Kleiman 1977). Mammalian mating bonds include cases where males mate with the same group (harem) of females (polygyny) and where males will mate with any receptive female and there is no continuing bond between individual males and females after mating (promiscuity). There are four forms of mate guarding: the defence of individual females during part or all of their period of receptivity; the defence of feeding territories overlapping the ranges of individual female or groups of females; the defence of particular group of females, during the mating season or throughout the year without the defence of any fixed area; and the defence of dispersed or clustered mating territories within a portion of the female range. In most species single males defend females, but in some cases several males cooperate to defend access to females groups or their ranges (Clutton-Brock 1989).

Nowadays, however, as we understand mating behaviour of various species better, we realize that 'typological' notion of a species is false and a variation in mating behaviour within population is common, particularly in ungulates (Lott 1991; Langbein 1999). Two most common ways to gain mating are by defending females (harem) or resources (e.g. forage). But these strategies are often accompanied with sneaking tactics and roving behaviour in harem-defence and satellite behaviour (when other males are tolerated within the territory to help defend it but gain very few matings) in resource-defence (Isvaran 2005). Also, individuals within population may display several tactics following the same strategy as they age or by their social status e. g. young or subordinate males attempt to sneak mate, but older or dominant males switch to defending harems (Clutton-Brock & Guinness 1982; Hogg & Forbes 1997); or

accordingly to the females availability: female-following where densities are low and switching to resource-defending where female density is high (Isvaran 2005).

Another strategy common in ungulates according to the condition of a male is making-the-best-of-a-bad-situation. As recent findings suggest in topi antelope (*Damaliscus lunatus*), alternative tactics can be explained by condition-dependent strategy influenced by body size (Bro-Jørgensen & Durant 2003). Males in poor condition and unable to succeed with more costly tactics may be forced to adopt tactics yielding low mating benefits, while larger males defend lek territories (Bro-Jørgensen & Durant 2003). Sometimes, the variation in mating behaviour is so diverse that it is difficult to distinguish between tactics and there is no clear indication whether the male defends resource-based territory, clustered mating territory or a lek territory (Isvaran 2005).

Most work on reproductive behaviour in ungulates has focused on male behaviour. However, female mating strategies and how it affects male mating tactics are needed to be considered as well. Considering the large female investment in parental care due to pregnancy, lactation and defence against predators, the fitness of female has been determined largely by their ability to provide resources and avoidance of predation for the female herself and her offspring (Clutton-Brock & Guinness 1982; Isvaran 2005). While males are often selected to accumulate their reproductive success within a relative short period, which favours dramatic traits but strong temporal variation in the intensity of selection, selection on females, although weaker at any point in time, may be more sustained in that the relative ranking of reproductive success among individuals is maintained long term (Stockley & Bro-Jørgensen 2011).

To understand a sexual selection it is required to consider both male and female mating strategies, especially since they are often strongly independent and coevolve in dynamic processes which involve sexual conflicts and cooperation.

2. 1. 1. MONOGAMY

In around 5 % of mammalian species, males are socially bonded to a single breeding female for life, in ungulates it occurs in some artiodactyls (Kleiman 1977). One of the theories is that the presence of a male improves the detection of predators and thus contributes to reproductive success of the pair (Dunbar 2013). There is some evidence that this could be the case in some monogamous antelopes; for example, in klipspringer (*Oreotragus oreotragus*), where predation rates are high, males and females alternate in watching for predators while their mate feeds and mates contribute to the early detection of intruders (Dunbar & Dunbar 1980; Dunbar 1985; Dunbar 2013). Females may test suitors by actively eliciting male competition and guarding ability in order to identify males with high competitive ability by scent marking at elevated rates. Such female mate screening is advantageous for superior male competitors, but conflicts with the interest of weaker suitor. The male klipspringer responds by over-marking the female scent to prevent detection of other males (Roberts & Dunbar 2000; Wong & Candolin 2005).

Almost all monogamous species show intrasexual territoriality (Mitani 1984). However, there is increasing evidence that individuals in some monogamy species mate outside of their pair-bond. Depending on the male range, which may cover the range of a single female, males may breed with a single partner (facultative monogamy), whereas where male ranges covers those of several females they may breed with several females (facultative polygyny). Because female range size varies widely within the species, the degree of polygyny probably differs widely between populations (Cockburn 1988; Brotherton et al. 1997). This occurs in species with limited availability of mates rather than by resources and predation. It emphasises benefits from male mate competition rather than from female mate choice (Davies 1991).

Facultative monogamy/polygyny occurs in a wide variety of animals including small ungulates like Kirk's dik-dik (*Madoqua kirkii*), where the pair maintains their territory marked by urine and dung. The offspring stays with its parents until another offspring is born (Jarman 1974; Barrette 1987; Brotherton & Rhodes 1996).

2. 1. 2. SINGLE MALE HAREMS

A) THE MALE DEFENDS HIS TERRITORY

In some species of mostly large herbivores, females live in social groups in ranges small enough to be economically defensible by a male, or where their ranges have well-defined core areas (resources like forage, water source etc.), males commonly defend the ranges or core areas of female groups as well as the groups themselves against invasions by other males. As the area occupied by female groups increases, the cost-effectiveness of territoriality declines and males are more likely to defend groups of females or wander in search of receptive females (Clutton-Brock 1989). Male defence of ranges or territories associated with polygyny extends over a large part of all the range of several females and is common in some of more sedentary ungulates, including camelids (Franklin 1983), cervids (Redford & Wemmer 1987) and some antelopes (Leuthold 1978; Gosling 1986).

B) THE MALE DOES NOT DEFEND A TERRITORY

If reproduction is strongly seasonal, males may compete intensely to defend temporary harems as in red deer, *Cervus elaphus* (Clutton-Brock & Guinness 1982). Although it is the most common tactic in male red deer, in some Spanish populations it has been reported as a tactic practiced alongside with resource-based defence. Carranza et. al. (1995) experimentally provided resources on an area in Spain and as a result, females concentrated at these resource areas followed by males switching from harem-defence to resource-defence which yielded greater reproductive success. In contrast, where breeding seasons are longer or reproduction is seasonal, harems are commonly defended throughout a year and competition is generally less intense. Harems of this kind are found in plains zebras (*Equus quagga*) and elands, (*Taurotragus oryx*). In some species harem groups regularly associate with each other to form larger herds (Hillman 1974; Klingel 1975; Hillman 1976).

Sometimes a harem group may include more than one adult male though a single male is usually responsible for most or all matings, as in waterbuck,

(*Kobus ellipsiprymnus*). Other males may benefit by attaching themselves to harems to reduce their own risk of predation and to establish social bonds with resident females by increasing the chance that they will be able to take over the harem group, while the dominant male may benefit from their presence as they contribute to defending the group or territory against intruders (Wirtz 1982).

This kind of mating strategy can be further divided into those where males join themselves to pre-existing groups of related females and those where most females leave their natal group and join particular males, as in zebra (Klingel 1975) and feral horses (*Equus caballus*)(Berger 1986). This difference appears to be connected with the risk of inbreeding to females; where females usually remain in their natal groups, the average reproductive success of individual males in particular groups is generally lower than the average age of females at first breeding, with the result that the risk to females of inbreeding with close relatives is low (Clutton-Brock 1988). Recent studies however have illuminated how sexual conflicts can operate at genetic level in ungulates. In red deer, fathers with high fitness sire daughters with low fitness generating a negative correlation between fitness variation in the two sexes (Foerster et al. 2007).

2. 1. 3. MULTIMALE GROUPS

A) MALES DEFEND THEIR TERRITORY

In some species (e.g. Equids), the group consists of several adult females with their youngs followed by reproductively active males who cooperatively chase and attack intruders within their home range. As females aggregate in large groups and their movement is unpredictable a single male may be unable to guard and mate with the whole group, so cooperative defence may have substantial advantages. Multimale groups usually consists of more than five breeding females, in some cases males spend part of their active time alone or in subgroups (e.g. bachelor groups) that range separately, but they follow female groups and defend receptive females directly. Multimale groups with spatial defence by males occurs in plains zebra, and feral horse (Gosling 1986; Clutton-Brock 1989).

Sometimes cooperation between females occurs in male-dominant societies as well. In feral horses unrelated mares reduce male harassment by forming stable bonds as a cooperative counter strategy. Mares improve their reproductive success by reducing harassment levels (Cameron et al. 2009).

B) MALES DEFEND A HAREM

In Cape buffalo, (*Syncerus caffer*) (Sinclair & AR 1977; Prins 1987), female groups are too large to be defensible by a single male, thus more than one male is commonly found in each group (Jarman 1974). In these groups males have established dominance hierarchy where dominance rank determines priority of access to receptive females (Prins 1996). As comparison to next chapter, 2. 1. 4., males do not defend territories covering the range of female groups against intruding males, though they commonly defend receptive females against other group members as well as against intruders (Clutton-Brock 1989). Bulls lose condition while they live in female herds and switch every few weeks between membership of mixed-sex herds and bachelor parties (Prins 1987).

A) A RESOURCE-BASED TERRITORY

Where females range over areas too large to be defensible and female groups are small or change in membership from hour to hour, males commonly defend mating territories smaller than the home range of female groups, sited in areas visited regularly by females in search for resources. These systems differ from those of type in chapter 2. 1. 2. a) in the male territory cover a small fraction of the female range and associations between males and particular females are usually temporary and unstable. These systems are common in antelopes (Gosling 1986), though they also occur in some cervids, antilocaprids, equids and white rhinoceros (*Ceratotherium simum*) (Kitchen 1974; Chapman & Chapman 1975; Owen-Smith 1977; Rubenstein & Wrangham 1986). In waterbuck (*Kobus defassa*), males defend contiguous territories with 30 to over 200 ha of grassland regularly used by female groups who range over an area three to four times the size (Spinage 2012). In species where resources favoured by females are more widely dispersed, as in Grevy's zebra (*Equus greyi*), male territories are often discontinuous (Owen-Smith 1977; Gosling 1986; Rubenstein & Wrangham 1986).

B) LEKS

Lekking is a behaviour where males defend tiny territories with no obvious resources in large aggregations used by female herds or visited by females solely for mating purpose (Clutton-Brock et al. 1993). In Kafue lechwe (*Kobus leche kafuensis*) clusters of very small territories, often less than 0.01 ha in size, are sited at the intersection of paths regularly used by females in their diurnal migration to feed at the edge of the floodplain (Schuster 1976). Lek formation is the result of cooperation between females and high-quality males, to both of whom the behaviour is mutually beneficial overall (Höglund & Alatalo 2014). According to indirect benefits model, females may prefer clustered males because high-quality males may defend the best territories, while territory size is smaller due to higher competition (Bro-Jørgensen 2003). According to the harassment avoidance model, females benefit from easier

defence of a small territory from harassing intruders by its owner (Clutton-Brock et al. 1993). Antipredator model shows, females initially benefits from mating at sites with good visibility and/or in clusters with safety-in-numbers benefits (Delm 1990).

The costs (fights, injuries etc.) are also higher, thus males of lekking ungulate species usually also adopt other mating strategies like the defence of resource-based territories, where they try to mate with females in mixed-sex herds, or intrude other males territories to force copulation with females present. Males on lek territories also tend to be much larger than resource-defenders and hence better suited to defend these high-benefit territories (Nefdt & Thirgood 1997; Bro-Jørgensen 2003).

The topi antelope developed a deception as an alternative manipulative tactic. In case of stalking predator, topi antelope alarm snort when the predator is detected, a territorial male often produce an acoustically similar snort when visiting oestrous females attempt to leave his territory. Females often respond to false snorts a move back towards the centre of the territory in precaution, thus the male often succeeds in mating (Bro - Jørgensen & Pangle 2010).

2. 1. 5. TEMPORARY GROUPS OR PAIRS

A) MIGRATORY HERDS

In a number of ungulates females aggregate in large, unstable, migratory herds, where the only stable groups are a female and her offspring. Dominant males may either defend receptive females or accept the presence of other males and attempt to maintain priority access to receptive females (Røed et al. 2002). These ungulates mate during the course of migration. This occurs in some populations of wildebeest(*Connochates taurinus*), topi and reindeer (*Rangifer tarandus*) (Espmark 1964; Gosling 1986).

B) ROVING MALES

In some species, females range widely and are solitary (nomadic) or live in small groups that are unpredictably distributed at low population density. These females have one or more seasonal home ranges but they are not considered as territorial with one exception during the first weeks of the calf's life when the cow-calf bond is the strongest (Franzmann 1981). Males range widely in search for oestrous females, consorting with them and defending them against other males (Gosling 1986) like in moose (*Alces alces*) (Peterson 1978). Roving males that guard only females in estrus are also found in a number of mountain ungulates, including ovids and caprids (Schaller 1977).

Many studies have examined reproductive fitness trade-off in females like the production, number and growth of offspring, but there is only a few studies examining fitness trade-offs of a male as quantifying of energy output in reproductive effort is not straightforward. To quantify male mating effort, some studies uses behaviours like reduced foraging, mate guarding or fighting frequency (Mysterud et al. 2004), other studies may use mass loss during the rut as a measurement (Forsyth et al. 2005).

In polygynous species, the mating success of a male is very dependent on intrasexual competition, therefore males may adapt different tactics. In bighorn sheep (*Ovis canadensis*), only dominant male defends (tends) a single oestrous female for up to 2 days (Hogg & Forbes 1997). During this period the dominant male displays courtship behaviour followed by repeated copulations accepted by the ewe. Only one ram tends to one ewe at time but tending ram can be replaced by more dominant ram. Fitness trade-off for this tactic is that tending ram spend more energy tending to the ewe then foraging, however only larger and heavier rams can afford to lose more mass during the rut in exchange to much higher reproductive success (Pelletier et al. 2006). Subordinate male develops an alternative tactic called 'coursing', where coursing male attempts to separate tending male from the ewe by engaging consort male into a physical combat, break his defence and force-copulate the ewe. Although coursing is less successful than tending, coursing males may obtain up to 40 % paternities in one season (Hogg & Forbes 1997; Pelletier et al. 2006).

2.3. ELAND (*TAUROTRAGUS ORYX*)

2. 3. 1. TAXONOMY

Kingdom: Animalia

Phylum: Chordata

Class: Mammalia

Order: Cetartiodactyla

Family: Bovidae

Subfamily: Bovinae

Tribe: Tragelaphini

Genus: *Taurotragus*

Species: *Taurotragus oryx* (Pallas 1766)

Subspecies   *Taurotragus oryx livingstonei* (P. L. Sclater, 1864)

Subspecies   *Taurotragus oryx oryx* (Pallas, 1766)

Subspecies   *Taurotragus oryx pattersonianus* (Lydekker, 1906)

2. 3. 2. ANATOMY AND MORPHOLOGY

The eland (*Taurotragus oryx*) is one of the largest African antelope together with the Derby (giant) eland (*Taurotragus derbianus*) (Underwood 1979). *T. oryx* has much shorter and more tightly spiralled horns, his ears are pointed and narrow, compared with more rounded and wide ears of the giant eland (Pappas 2002). Shoulder high ranges 125 - 160 cm for females and 135 – 178 cm for males. Body mass averages 300 – 600 kg for females and 400 – 942 kg for males (Kingdon 2015), but even with such massive body its enclosure has to have high fences because elands can jump over 2 m high fences quite easily. Throughout their lives, males tend to increase

in weight. Their neck and shoulders darken from tan to grey and the dewlap enlarges until it hangs like a curtain up to below the knee level. The hair on their forehead and nose changes its length and becomes bushier (Kingdon 2015).

Eland has 2 – 15 transverse white stripes which pattern is individually unique. Colour of coat varies from dark grey brown to reddish brown and males tend to turn blue-grey as they age (Hillman 1976). Coat colour and prominence of stripes vary throughout distributional range and among subspecies. It is lighter and stripes are less visible on animals in southern area of their range, compared with animals in northern areas (Skinner & Smithers 1990). All eland have a black spot on the posterior upper region of the forelegs and a dark dorsal stripe running down the back (Posselt 1963). The side, or 'false', hooves on the hind legs are embedded in glandular patches which presumably leave scent trails (Kingdon 2015). Both sexes have spiralled horns, horns of males are shorter, thicker and more pronounced spirals, their length averages 54 cm (43 – 67 cm). Horns of females are longer, thinner and average 60.5 cm (51 – 69.6 cm) (Estes 1991).

As the male's weight continuously increases, his coat changes colour and his dewlap grows progressively as he ages and grow in size probably the largest part of his life. The dewlap might have tactile and thermoregulatory functions (Kotrba et al. 2007) but the continuous enlargement of its silhouette with age suggests that it is a device to increase the impression of size in neck and shoulders and the differential colouring of the forequarters also serves this end (Kingdon 1982).

Common eland live in approximately one-third of Africa. Originally from Cape to forest margins in the Zaire basin, Nile floodplain and arid North Kenya (Figure 1) (Kingdon 2015). According to The IUCN Red List of Threatened Species it is classified as an animal with least concern (Group 2016). Eland occur in savanna, woodland, open grassland plains, and montane grassland with wide variety of flowering plants but avoid densely wooded forests (Rowe-Rowe 1983).

FIGURE 1 GRAPHIC DISTRIBUTION OF ELAND (BY THE IUCN RED LIST)

Teeth, jaw muscles and digestive system are all adapted to a high-protein, low-fibre diet (Kingdon 2015). They have been classified both as intermediate feeders preferring forbs along with foliage or shrubs and trees and as browsers that have adapted to grazing (Hofmann & Stewart 1972). Eland's diet consists of common trees and shrubs, including *Accacia, Combretum, Commiphora, Diospryas, Grewia, Rhus* and *Ziziphus.* They also eat forbs from the family Compositae, including *Acanthospermum, Bidens, Tagestes* and *Tarchonantus sp.,* and fruits from genus *Securinega* and *Strychnos* (Kingdon 1982; Skinner & Smithers 1990). They also eat grasses of genus *Setaria* and *Themeda* (Hillman 1976)*.* Eland graze during the rainy season, when grasses are plentiful but browse more during dry winter months. Forbs are eaten in summer and winter months an addition to grasses and browse (Rowe-Rowe 1983). There is a sexual difference in the amount of grass taken during the wet season, because males venture less into the open country than the females, their diets remain more constantly one of browse and herbs (Hillman 1976). Although eland drink when there is enough water, they obtain most of it from their diet (Skinner & Smithers 1990). Eland also commonly visits salt licks and can climb as high as 5,000 m for sodium licks near snowline on Kilimanjaro (Kingdon 1982).

Although it is an African ungulate, eland has no problems to deal with European climate winter conditions. A study using thermal camera to compare coat temperature of eland and dairy cattle suggested that eland is able to prevent heat radiation as well as dairy cattle even in temperatures close to 0°C (Kotrba et al. 2007).

Young animals, especially females, are highly nomadic, elder animals, especially males, are more residential. Thus, home ranges have been found to vary from 200 to 1,500 km^2 (Bothma & Van Rooyen 2005; Kingdon 2015).

Eland is resistent to trypanosomiasis which is transmitted by flies (Posselt 1963) but are not resistant to theileriosis, a bacterial disease transmited by a ticks of genus *Rhipicephalus* (Young et al. 1980). In comparism to catle, eland is often asymptomatic or show only mild symptoms when infected (Young et al. 1980).

Females reach sexual maturity in approx. 2.5 years of age, and males start to be accepted as mates at 4 years of age (Hall 1975), however in captivity males start to be fertile in ca. 2 years of age and females can conceive at the age of 15 months (personal communication, October 10, 2016). They can reproduce at any time of the year, however more matings had been recorded in Africa during rainy season, leading to birth peaks nearly 9 months later at the end of dry season (Kingdon 2015). Estrus occurs in 21 to 26 – day intervals and lasts for 3 days (Posselt 1963). During the peak of the heat, the cow gets into the torpor to accept the bull's mating attempt (Figure 4, Appendices) and the bull jumps a bit when ejaculating (Figure 5, Appendices)(personal communication, October 10, 2016). Gestation is 271 ± 2.9 days and parturition usually takes place at night in Africa (Skinner & Van Zyl 1969). In captivity gestation length is shorter, 259.7 ± 1.8 days (Hubmer 2011).

Females become very restless before calving and shows interest in other calves and in birth fluids of other females. During delivery she lays down and stands up shortly after delivery. Early maternal interactions involve nose thrusting, licking, chewing and a variety of vocalizations by both mother and calf (Underwood 1979).

At birth, male calves weight 30 ± 1.3 kg, and female calves weight 25.5 ± 0.7 kg (Skinner & Van Zyl 1969). The young have a brief lying-out period before they join the group. It is during these two-weeks of concealment that a calf is totally dependent on their mother. After this period, allosucking was observed (when a calf drinks from another female and not its mother) and the mother's role as a companion is supplanted by the other young animals in the nursery group (Kingdon 1982). Calves mimic their mothers' browsing behaviour almost immediately postpartum, but nursing is the primary form of feeding, they are weaned by 6 months of age (Underwood 1979). Growth rates are exceptionally fast thanks to extreme richness of eland milk (Kingdon 2015).

Eland is crepuscular and feed in early morning and in the evening (Kingdon 1982). They are powerful animals and superb jumpers. Young eland can clear 3 m high fences from a standing position (Hillman 1976). Unlike many antelope, eland lack territorial behaviour (Underwood 1981).

They are social and occur in large herds of hundreds of animals. Groups however may be of one sex only or consists entirely of half-grown (Shortridge 1934). Hillman (1974) has pointed out that not only do the young tend to associate in large numbers but that all herds with young are considerably larger and has suggested that this evolved as a defensive tactic against predators. It lies in the intense mutual attraction of calves to other calves than to their mothers. They also groom and lick one another more, whereas adults have minimum physical contact (Kingdon 1982).

Some of the older males tend to be less nomadic than others. Adult bulls are found in numbers exceeding six or seven, it is because in smaller group it is easier to establish the relative rank than in larger group where an extended hierarchy is required and it is more likely the males are closely matched and therefore intolerant antagonists (Kingdon 1982).

The cows are hierarchical as well. Fights between females are rare but violent and the outcome is settled almost immediately. When the herd bunched against a cheetah it is the lowest ranking cow who is forced on to the periphery (Hillman 1976).

Both sexes tend to rub their foreheads in muddy puddles after a storm. Males rub their foreheads in their own urine to increase their attractiveness almost every time they urinate and Hillman (1974) observed one male rubbing his head in elephant's urine. The hair on the bull's forehead gets thickly covered by the mixture of mud and urine, which after drying may puff out as a little dust cloud as the animal shakes its head. The bull also soaks his forehead in an oestrous cow's urine probably to be less intimidating and more familiar to the cow (Kingdon 1982).

Ungulates use many posture and movements for communication (Kiley-Worthington 1976). They have a well-developed repertoire of visual signals, which were placed in three categories such as 'aggressive', 'sexual' and 'fearful'. But this approach has considerable disadvantages. It makes assumptions concerning internal motivational states and thus there can be several arguments. For example head extended by male may be seen to occur during courtship in many ungulates, thus it is usually associated with sex and it may be assumed that the male performing head extension is sexually aroused. However the head extension is often seen in many other situations performed by either males or females (for example to sniff something new). Such movements and postures are thus hard to categorize because many do not fall into single category (Treus & Kravchenko 1968; Kiley-Worthington 1978).

For my study I selected several examples of visual displays that may occur during mating and courtship.

a) *Flehmen* – Involves pronounced extension, elevation and partial inversion of the upper lip, the lower lip is not lowed. The head is raised and extended forwards. It usually occurred when an animal had smelt or tasted the urine of another animal. It is common after an oestrous female had urinated (Figure 7, Appendices).

b) *Head rubbing* – When itching around the head or neck, the eland will rub itself on a convenient surface. It also occurs around the time of the rut (in males) and parturition (in females). Males often rub their head in any wet patches on the ground, including those formed by rain or water. Flehmen is elicited by the urine of another animal, whereas head rubbing to the animal's own urine. This suggests that flehmen is a taste-testing activity and head rubbing is more egocentric self-marking activity.

c) *Sniffing* – Movement of nostrils, usually associated with head movement. This is used for visual communication at short range (Figure 8, Appendices).

d) *Head extend* – A common posture whenever eland investigate a strange object or to smell another animal. It is also associated with courtship. Before mounting the male eland performs a rather stereotyped variation of this posture. He holds the head extended and slightly up in order to clean the female's back, lip-licks, and often vocalises with a quiet "mm". Simultaneously he runs at the female with short strides. If she stands long enough before leaping forward, he mounts and may achieve intromission. Intromission and ejaculation occur very rapidly (when the male ejaculate he jumps up a little), the whole sequence takes around 5 secs.

e) *Head tossing* – Head extend forwards followed by the head being thrown over the body – sometimes the horns touch the back. It is particularly characteristic of females and occurs as a reaction to irritation from flies, or in particularly non-social situation when awaiting food, or when a male is attempting to mount a non-receptive female.

f) *Head shaking* – Consists of a lateral movement of the head which is repeated rapidly. Females perform more than males. It is often interpreted as a threat (38 %).

g) *Tail withdrawal* – Protective tail withdrawal occurs when the animal is being chased, and about to be spiked by a horn in the rump. It is usually accompanied by leaping forward with vigour. It also occurs in a non-receptive female when mounted by a male.

h) *Head turning* – This movement has the effect of stopping the approaching animal (69 %) and is often performed by females in estrus to approaching or closely following males.

i) *Head lowering* – Involves movements and postures of whole head and neck below the horizontal line of the back. It is restricted to social situations, it is characteristic particularly when an individual's distance has been violated and it is interpreted as a threat.

j) *Head pointing* – A slight lowering of the head accompanied by the drawing of the chin, so the horns are pointed towards adversary. It is described as an intention movement to spike, and is interpreted as a strong threat.

k) *Following* – The bull persistently follows and circles the cow

l) *Play-fighting* – Eland fighting method of choice is wrestling, they entwine their horns and then by pushing and rotating the head using the horns as levers, put very considerable pressure on their opponents. The difference in fight and play-fight is in the vigour with witch the fight is conducted (Figure 2)(Kiley-Worthington 1978).

FIGURE 2 WRESTLING (KOTRBA 2005)

3. AIMS OF THE THESIS

The main aim of this study was to describe and analyse behavioural repertoire during reproduction of eland through analysing video recordings and to estimate the length of gestation based on recorded copulation.

Because, there has not been quantified reproductive behaviour of eland yet we predicted how behaviour of male and female would influence length of copulation and time between copulations. We proposed and tested hypotheses based on empirical experience with elands:

1) The length of copulation will be positively influenced by behaviour of the male prior to copulation and by response of the female during copulation.

   I predicted that:

   a) Copulation will last longer if the male will express more times woo behaviour prior to copulation and the female will freeze and accept copulation more readily.
   b) Copulation will last longer if the male will express more different woo behaviour prior to copulation and female will freeze and accept copulation more readily.
2) The copulation will last longer when the female actively express readiness for copulation by initiation of wrestling with the male prior to the copulation.
3) The time between consecutive copulations will be longer in case:
   a) Male will express more times woo behaviour prior copulation and female will freeze and accept copulation more readily.
   b) Male will present different woo behaviour prior to copulation.
   c) Female will freeze and accept copulation more readily.
   d) Female will actively express readiness for copulation by initiation of wrestling with male prior copulation.

4. MATERIAL AND METHODS

The study animals were maintained at the Czech University of Life Sciences Prague CULS Farm Estate Lány, located 35 kilometres West from Prague on the edge of Křivoklátsko Protected Landscape Area. The University Farm has been involved in farm breeding of eland since 2006. On average, there are 50 heads of the animals on two hectares.

From previous studies there were industrial cameras (Sony 760H Super HAD CCD II equipped with infrared 'night' vision ability to provide video feed during nights) installed in the stable (Figure 9, Appendices), which were recording continuously 24 hours, 7 days per week for duration of one month: October 2013 and June 2014 with the first male (4 – 5 years old); and September 2014 with the second male (7 years old) (Figure 10, Appendices). For my study I used 4 cameras placed above the barn so I could have a clear vision of everything that was happening in the monitored area. Males and females were kept separately prior to our monitored period, when one breeding bull was introduced to the group of 9 females to mate. All animals were marked by individual ear-tags.

The group had access to 230 m^2 of barn area (Figure 11, Appendices) and a free access to water and feed which was *ad libitum*. Based on dry matter, the feed mixture consisted of corn silage (52.1 %), lucerne (alfalfa) haylage (26 %), meadow hay (10.4 %), straw (10.4 %) and minerals (1 %).

Video recordings were obtained during routine housing system when male and females are in one group with only exception, that male was introduced in the herd of females after all calves were born or weaned, to synchronise next calving. Male spend time prior this period in group of youngsters and other males.

Recordings on reproductive behaviour were then analysed in behavioural coding and analysis software Observer XT 10 (© Noldus Information Technology, Wageningen, Netherlands). By comparing dates of mating and dates of calving, the length of gestation will be found.

Observations were focused mostly on male as I defined expected behaviour.

1. Tactile point displays with defined place (considered as woo behaviour)

   a) Licking: the male licks the coat or genital of the female

   b) Rubbing: the male rubs his chin and/or neck against the female (Figure 8, Appendices)

   c) Lean on: the male leans his head on the female's back or neck

   d) Lick or sniff: the male licks or sniffs part of the female body (sometimes due to the video quality it was difficult to tell exactly which)

2. Movements with horns

   e) Head-butting: horn pointing with a slight nudge

   f) Wrestling: play-fighting/wrestling (considered as woo behaviour) (Figure 2)

3. Interaction of other female

   g) Jumping: another female mounts the male or the female

   h) Sniffing: another female sniffs the female during courtship or mating

4. Mounting (Figure 4, Figure 5, Appendices)

   i) Copulating: the male mounts the female (I identify successful mounting, when the female freezes; unsuccessful mounting, when the female runs away; copulation with and without ejaculation)

5. Moves of the male

   j) Walking around: the male walks around standing female from side to side (considered as woo behaviour)

   k) Flehmen: the male stands with his upper lip extended, elevated and partially inverted (Figure 6, Appendices)

   l) Retreating: the male retreats from the female.

As I got the exact date of copulations, each female was identified and after the parturition I could calculate the precise length of their gestation.

Descriptive statistics including plots were done in programme Statistica (Dell Inc., Tulsa, Oklahoma, USA). All analyses were performed using statistical software SAS System V 9.4 (SAS Inst. Inc., Cary, NC, USA). Data normality were assessed by plotting histograms and normal probability plots. Four different tests were performed (Shapiro–Wilk, Kolmogorov–Smirnov, Cramer–von Mises and Anderson–Darling). 'Length of copulation' and 'time between copulations' were included as a dependent variables in analyses. To fit the skewed distribution of data on 'time between copulations' into a normal distribution root4 transformation was applied. Each dependent variable was analysed separately using the Generalized Linear Mixed Model (GLMM). The explanatory variables included in analyses were categorical of 'behaviour of female during copulation' with two levels (freeze and moving away), 'number of woo episodes before copulation'- including precopulative behaviour of licking, sniffing, rubbing, head-butting, walking around and wrestling, 'number of woo types expressed before copulation' and if 'female initiated wrestling' with two levels (yes or no) before copulation. To account for repeated measures on the same animals over the experimental period, analyses were performed with PROC MIXED, using the individual female as a random factor. Differences between the effects were tested using the F-test. For multiple comparisons, I used the Tukey-Kramer adjustment.
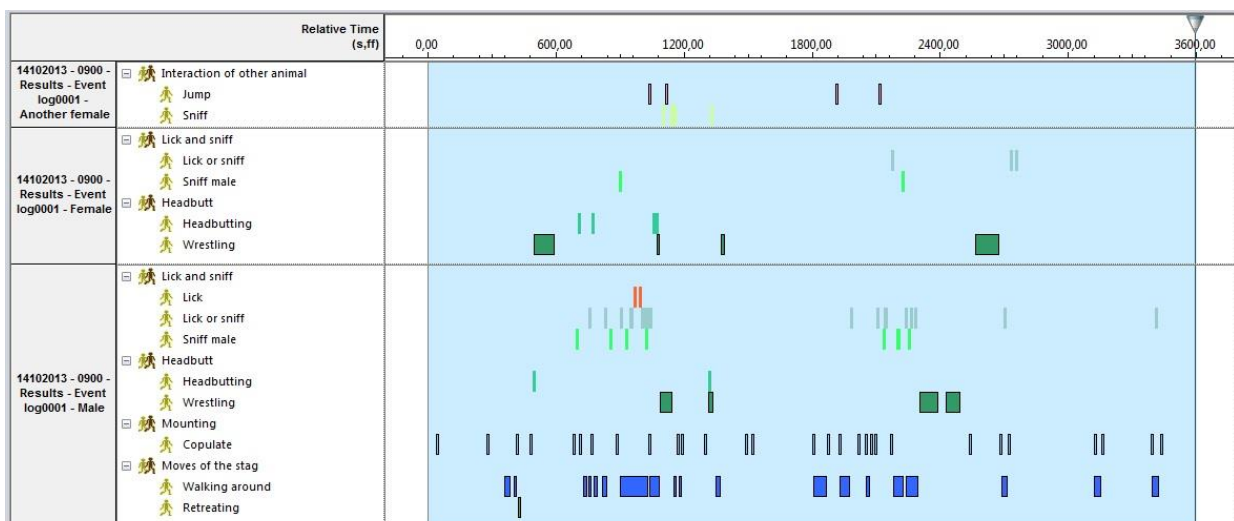

FIGURE 3 VISUALISATION OF ANALYSED DATA

5. RESULTS

In total, 599 episodes of behaviour linked to reproduction was extracted from 2,232 hours of video recorded of elands after the introduction of the male into herd of females and processed. It covered together three mating seasons, each of one month recording. During my observations I recorded together 95 copulations. These copulations were preceded 13 times by light head-butting initiated in 85 % (n = 11) cases by the female directed in 60 % (n = 7) cases toward male's head/horns, in 20 % (n = 2) cases toward male's side and in 20 % (n = 2) cases toward male's rear. The male lean on female's back in 2 cases. The male licked or sniffed the female totally in 132 cases which was on neck (40 %, n = 53), on genital area (35 %, n = 46), on head (17 %, n = 23), on back (6 %, n = 7) and on rear (2 %, n = 2). In 95 cases the male rubbed female on back (68 %, n = 65), on neck (20 %, n = 18), on side (7 %, n = 7) and on rear (5 %, n = 5).

Daytime did not play much role in frequency as 'mating episodes' were distributed during the day 6 am – 6 pm in 60 % of copulations and during the night 6 pm – 6 am in 40 %.

'Length of copulation' (Figure 12, Appendices) was not influenced by any of explanatory behaviour, namely by 'behaviour of female during copulation' ($F_{(1,78)}$ = 0.93, P = 0.34), 'number of woo episodes before copulation' ($F_{(14,78)}$ = 0.79, P = 0.68), 'number of woo types expressed before copulation' ($F_{(4,78)}$ = 0.24, P = 0.91) and also not by female's activity'female initiated wrestling' ($F_{(1,78)}$ = 1.27, P = 0.26).

'Time between copulations' was influenced by 'behaviour of female during copulation' ($F_{(1,78)}$ = 5.95, P = 0.017) with longer time between copulations when female was running away as male tried to mount her. Also interaction between 'behaviour of female during copulation' and 'female initiated wrestling' ($F_{(2,88)}$ = 4.87, P = 0.009) influenced 'Time between copulations', but not 'number of woo episodes before copulation' ($F_{(14,78)}$ = 1.47, P = 0.141), 'number of woo types expressed before copulation' ($F_{(4,78)}$ = 0.17, P = 0.243) and not 'female initiated wrestling' ($F_{(1,78)}$ = 0.17, P

= 0.684). Mean 'time between copulations' when she freeze was 91.7 ± 15.1 s (mean ± st. error) in comparison to when she moves away was 136.4 ± 19.1 s.

Mean 'time between copulations' when female did not initiate wrestling with male before copulation and freeze during copulation was 72.5   ± 16.3 s (mean ± st. error) in comparison to when she did not initiate wrestling with male before copulation and moved away during copulation was 136.8 ± 18.4 s. The longest mean 'time between copulations' was in situation when female initiated wrestling with male before copulation and freeze during copulation (156.6 ± 30.3 s; mean ± st. error).

Length of pregnancy from 13 females parturition was calculated to be 273.53 ± 2.33 days (mean ± SD).

6. DISCUSSION

Expectation was that the length of copulation would be influenced by behaviour of the male prior to the copulation. As male shows more woo behaviour, female might then intensified her willingness to accept male for copulation and freeze which can prolong copulation. This was the case for eland, because the length of copulation was not influenced by any explanatory behaviour. However 'woo behaviour' like licking, rubbing and following of the female plays an important role, because the male tests receptiveness of the female and hence determines success of the copulation (Kiley-Worthington 1978).

During this study I observed two different males. The first one, who was 4-5 years old at the time of my study, displayed most of the described pre-copulation behaviour (Treus & Kravchenko 1968), the second one, who was 7 years old, did mostly only flehmen and tasted urine of females without displaying more tactile 'woo behaviour' or this kind of behaviour was very scarce, though. According to Isvaran (2005) males tactics commonly change with their age, size and condition, where young males adopt sneaking and harassing tactic to try to mate, sometimes forcibly, whereas adult males adopts tactics such as harem-defence or territory-defence. However Kingdon (1982) suggests, that bigger, greish bulls with more developed dewlap and longer tuft indicating their age and dominance, are more attractive for the females. Thus younger male has to invest more effort into the seducing than older, more mature, bull. Unfortunately I did not collected enough representative data from the second male that would influence further data analysis, thus further research regarding different males approach would be necessary.

According to several authors gestation length differs: 259.7 ± 1.8 days in Lány (Hubmer 2011), 271 ± 2.9 in Africa (Skinner & Van Zyl 1969) and 270 – 280 days in Askaniya-Nova (Treus & Kravchenko 1968). From my study of 13 females that gave birth after copulation during observed periods the gestation length was 273.53 ± 2.33 days. Nevertheless Skinner and Van Zyl (1969) suggest that there is a difference in the gestation length according to the biotope where the group of elands live. In higher situated savannah with 'temperate' climate and relatively high rainfall (380 – 800 mm)

during summer, prolong the gestation length (279±4.9 days) than in shrubs savannah with subtropical climate and lower rainfall (150 – 400 mm) during summer where the gestation length was shorter 265 ± 2.7 days. My results coincide with results in 'temperate' part of Africa as CULS Farm Estate Lány is situated in temperate climate of central Europe, however it differs to results from previous study in Lány. But my study was done during several months (and seasons: October, June and September) so my results might be influenced by different seasons or by diet which has been the same with same nutritional value thorough year.

As a part of courtship behaviour, I observed play – fighting or wrestling between copulations and as my results confirm, wrestling was initiated by the female when she was on the peak of the heat and froze during the copulation. However Kiley-Worthington (1979) in her study refers to wrestling as a play-fight among young animals or as a fight between two same-sex animals and as a display of a courtship behaviour between the bull and an oestrous cow.

7. CONCLUSIONS

Reproductive behaviour, i.e. mainly copulation length and time between successful copulation was studied in nine females of farmed common elands (*Taurotragus oryx*) during three mating periods. There was not effect of male and female behaviour prior copulation and female during copulation on length of copulation which lasted 4.08 ± 0.63 s (mean ± SD). Time between successful copulations was influenced by the behaviour of the female during the copulation, when the female froze the mean time between copulations was shorter in comparison when she ran away (91.7 ± 15.1 s vs. 136.4 ± 19.1 s, mean ± SD). Length of pregnancy from 13 females was 273.53 ± 2.33 days (mean ± SD), what was different from indirect studies based on hormones. It was not possible fully to evaluate reproductive behaviour of different males with different qualitative traits which might be of interest for future studies not from only scientific point of view, but also from practical breeding one.

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FIGURE 4 MATING (KOTRBA 2005)

FIGURE 5 COPULATION WITH EJACULATION (KOTRBA 2005)
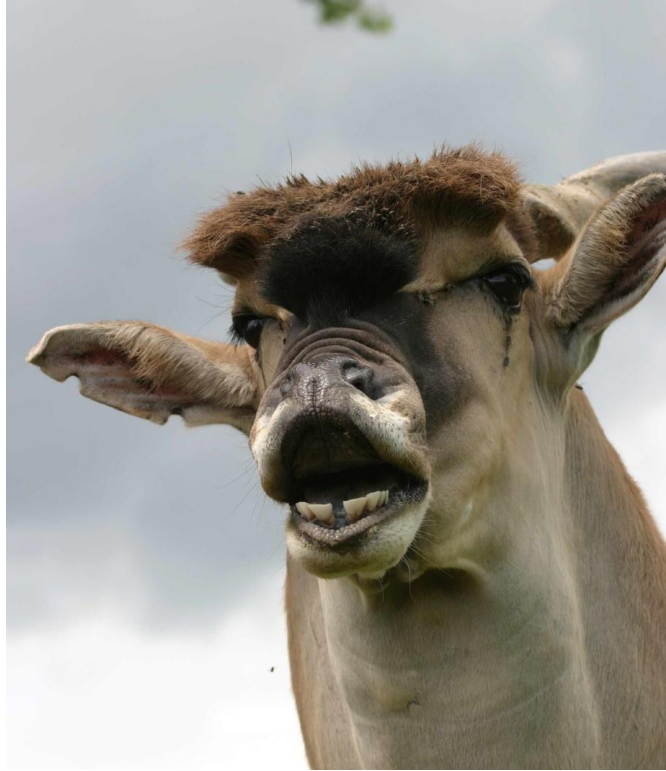
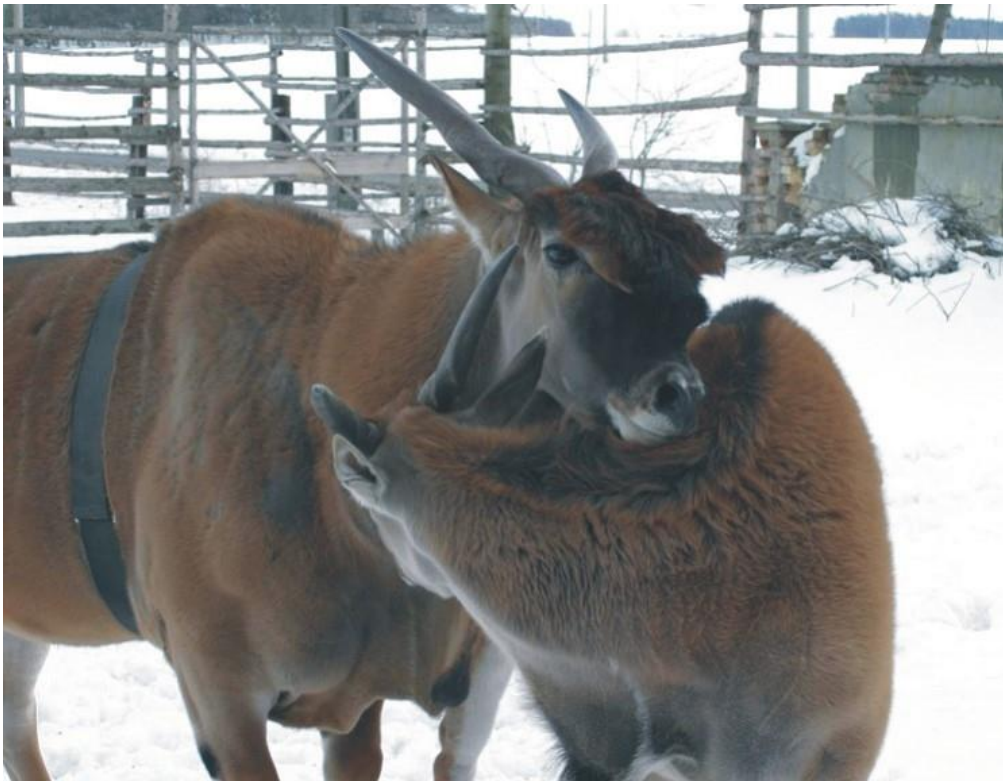FIGURE 6 FLEHMEN (KOTRBA 2005)

FIGURE 7 SNIFFING/RUBBING (KOTRBA 2005)

FIGURE 8 CAMERA IN THE BARN (TAMCHYNOVÁ 2014)

FIGURE 9 2ND MALE HANNO (TAMCHYNOVÁ 2014)
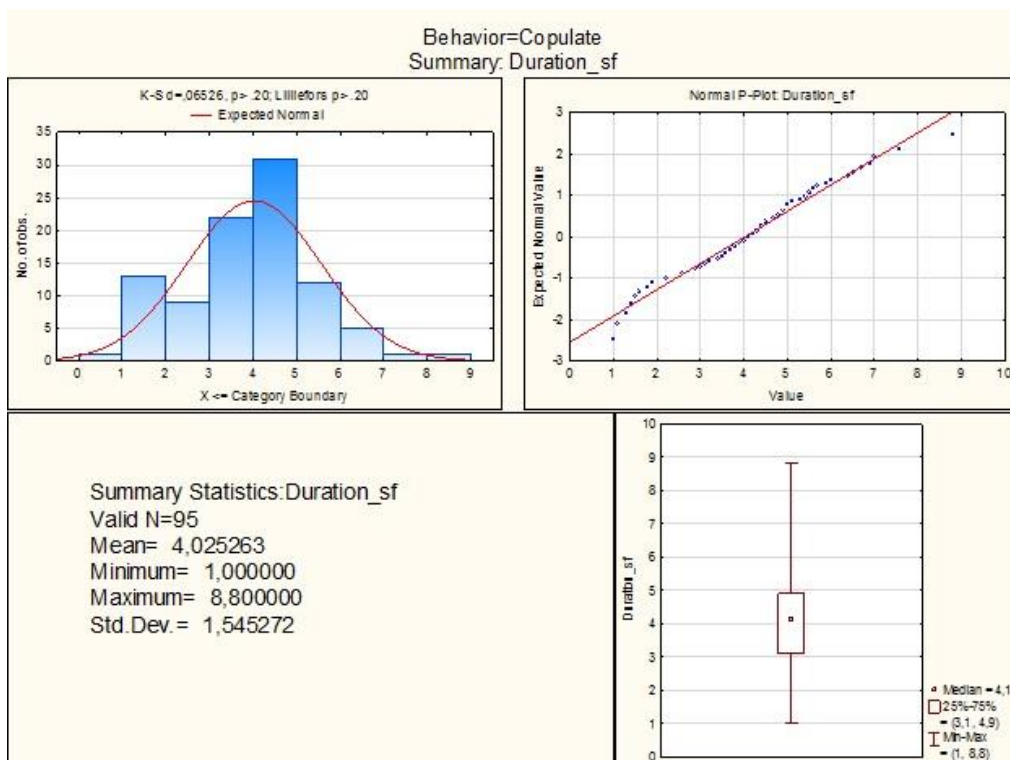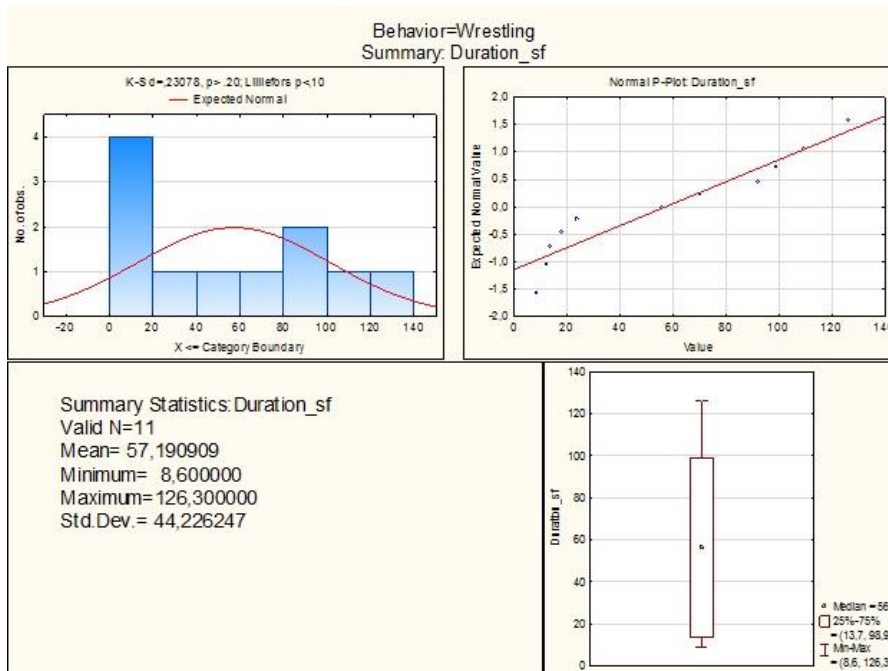
FIGURE 10 THE BARN WITH FEMALES

FIGURE 11 LENGH OF COPULATION

FIGURE 12 LENGTH OF WRESTLING