CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE

Faculty of Tropical AgriSciences

Department of Animal Science and Food Processing

Social Structures among Different Groups in Common Eland

Master Thesis

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DIPLOMA THESIS ASSIGNMENT

María Martínez Valdeolivas

Wildlife Management in the Tropics and Subtropics

Thesis title

Influence of dominance rank in the quality of horns in farmed eland

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Objectives of thesis

The aim of this thesis is to understand the social hierarchy structure of the species and its relationships with horn growth both in males and females.

Methodology

Common Eland (Taurotragus oryx) is a social antelope living in herds of 25 to 65 animals in the wild. The data collection will begin in February 2014 and will end in February 2015. During two days per week, every second week, the interactions between the animals will be observed and recorded. The hierarchy and social relationships will be studied in the 35 individuals hold in the CULS experimental facilities in Lány. Animals will be divided in diferent groups along the study period, and this group compostition will change every 2-3 months because of handling routines, but also in order to analyze as many variants of social group as possible (different group sizes and different composition: adult males, aldult females, mixed groups, bachelor groups...). To study the hierarchy in the herd, we will use specific softwares for dominance analysis (DomiCalc, SOCPROG...). Data collection will be done by direct observation of the animals and video recording. Body characteristics such as weight and horn size will be measured in several moments along the season. Since some animals will be culled along the study period, these will be subjected to a deeper analysis of horn quality, including detailed analyses of horn chemical composition and mechanical properties.

The proposed extent of the thesis

ca. 40 pages

Keywords

Animal behavior, Taurotragus oryx, hierarchy, horn, Common Eland

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DECLARATION

I hereby declare that this Dissertation entitled "*Social Structures Among Different Groups In Common Eland*" is based on my own work. All colleagues collaborating in my research activities, and the funding sources for the research here presented have been quoted and acknowledged.

In Prague, 24 April 2015.

María Martínez Valdeolivas

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ABSTRACT

Social Ungulates form different kinds of group structures in the wild, which frequently change in size and composition along the year. In this thesis, the common eland was used as animal model to study the behavioural patterns among these different social groups. Social relationships in thirty-two groups of farmed elands were studied. These groups were based on three main social structures: females-based groups, males-based groups and mixed groups. In all the group structures, the most frequent social interaction observed was based on dominance displays. Nevertheless, female-based groups were less aggressive than male-based groups, while these present a strongest linearity probably linked with the access to female. Differences were found in the occurrence of certain displays: females use yield in high frequency, while males displayed wrestle more frequently. This is in agreement with the expected function according to their horn dimorphism. All the studied group structures showed to have a linear hierarchy according to Landau's index and triangle transitivity. Moreover, these behavioural differences lead to the existence differences in the strength of Landau's linearity index (although these differences were not reflected by the triangle transitivity).

1. INTRODUCTION AND LITERATURE REVIEW

1.1.   COMMON ELAND

The common eland [*Taurotragus oryx* (Pallas, 1766)] is an endemic antelope from South-East Africa (Fig. 1). The species belongs to the family Bovidae*,* and the tribe Tragelaphini*.* Three subspecies are currently recognized; *T. o. oryx* in southern Africa, *T. o. livingstonii* (Sclater, 1864) in East-Central Africa and *T. o. pattersonianus* (Lydekker, 1906) in Tanzania (Groves *et al*., 2011).

Figure 1. Current distribution of the common eland in the wild (extracted from IUCN, 2008).

The common eland is the second largest African antelope; being the biggest the giant eland (*T. derbianus*). In common eland the shoulder height averages from 163 cm in males to 142 in females, while body mass averages from 500–600 kg for males and 340–445 kg for females (Pappas, 2002). Elands are large cow-like animals, with spiralled horns in both sexes. The pelage is tawny with short hairs, becoming blue-grey with age, especially in males. There are variable white stripes on the back and flanks. Males present a long thin

pendulous dewlap, while in females it is smaller and thicker (Groves *et al.*, 2011). Sexual dimorphism is reflected on the horns; females have thinner and longer horns, ideal for delivering quick stabs, while male's horns are shorter and thicker, better for wrestling, which is also facilitated by the muscular development of the neck and shoulders (Kiley-Worthington, 1977).

Common elands occupy a wide variety of habitats; using open plains, savannahs, and lightly wooded areas (Pappas, 2002). They are not found in deep forests, in true deserts, or in completely open grassland, though they do occur in grassland with a good herb cover or which is interspersed with browsing habitat along drainage lines (Groves *et al.*, 2011).

The common eland has been classified both as intermediate feeder, preferring forbs along with foliage of shrubs and trees, and as browser that have adapted to grazing. Elands graze during the rainy season (October-April), when grasses are plentiful, but browsing increases during the drier winter months (May-September; Pappas, 2002). Common elands are unusual among browsing bovines since they move long distances in search of ephemeral food sources. They have other attributes that are more typical of grazers such as an open social system. This life-style allows common elands to exploit a resource that is not available to other browsers: bushy vegetation and herbs sparsely scattered in the grassland. In the Kalahari Desert, the only other large browsers (greater kudus, *Tragelaphus strepsiceros*) are confined to patches of thicker vegetation, while common elands move freely through the system, and make use even of dune areas where the only bushy vegetation consists of dwarf shrubs. Diet usage has been associated with habitat use; they show a preference for bushy habitat during the dry season and for grassland

in wet periods. Common elands are able to select a diet low in fibre content by eating young shoots of woody species and by consuming large proportions of palatable woody species with low fibre content. Feeding takes place from ground level up to 2 meters, using their lips rather than their tongue to grasp food (Groves *et al.*, 2011). Common trees and shrubs in their diet include Acacia, Combretum, Commiphora, Diospyros, Grewia, Rhus, Ziziphus, Acanthospermum, Bidens, Tagestes, and Tarchonanthus, but also fruits from Securinega and grasses as Setaria and Themeda (Pappas, 2002). Adaptations to a mobile life include the ability to deal with prolonged periods without water. While they will drink when water is available, they are also able to obtain sufficient moisture from the food. They also have physiological adaptations that allow them to survive without drinking. Their body temperature may increase from 33.9 to 41.2ºC. The excess of heat accumulated during the day is dissipated at night though conduction and radiation, and in order to reduce the water loss at night elands breathe more slowly and deeply. They have a very high metabolic rate considering their size and excrete great amounts of urea in their urine. Although common elands are sizable animals they are capable of moving a great speed. The gallop generally develops into a fast trot, which can be sustained for a considerable time. They are remarkably good at jumping, and can easily clear a two-meter high obstacle (Groves *et al.*, 2011).

Females reach sexual maturity around 2.5 years old, while males reach it at 4 years old (Hall, 1975; Hosking and Withers, 1996). This disparity of puberty onset between sexes may be ensuring that calves born in the same year will not breed. There seems to be a peak in the calving season around August to November in southern Africa, but copulation and calving has been reported at all times of the year in captive settings. Gestation lasts around 9 months (271 ± 2.9 days), and elands carry a single calf per pregnancy. This species can live up

to 25 years. The observed oestrus cycle length and time between copulations, is 21 to 26 days, with oestrus lasting approximately 3 days. Females can exhibit oestrus as soon as two weeks after parturition, but rarely conceive during this interval. This may be related to the fact that calves are weaned around 6 months of age (Pennington, 2009).

1.2.   SOCIAL STRUCTURE

In the wild, common elands have a very fluid structure, group size varies from solitary animals to groups of several hundred (Hillman, 1987, 1988) and there appear to be no stable long-term relationships between individuals (Groves *et al.*, 2011). The most common long-term associations are those between a female and her calf (for as long as suckling lasted), and possibly that among young animals while they are part of the nursery group, up to two years (Hillman, 1987).

Hillman (1987, 1988) describes that adult groups are usually small in size, especially when comprised of one sex only (groups of one sex only were about three to five individuals and around twelve when the group was mix). Group containing juveniles in addition to adults are much larger, while those with calves are very large, often numbering over 100 eland where the environmental conditions allow it. Individual elands move freely between groups. Males spend much of their time in multi-male groups; even in the presence of oestrous females, association between individual elands is minimal, rarely lasting more than few days. The same eland individuals, however, can be seen together again after relatively long periods of time. The eland demonstrates a social organization typical of the Tragelaphini, but that is modified by its much larger body size compared with other

members of the tribe, and its seasonal occupation of open grassland habitats. It seems likely that the aggregation of adult females in large number in the presence of juveniles is linked to their association with their calves, which in turn have aggregating tendencies with their peers. Calves are physically attracted to each other and frequently stay in close proximity, even lying and standing touching each other. More individuals gather together in nursery groups when the environmental conditions improve, but this is not true with groups of adults. This suggests that the limits to the size of juvenile aggregations are set by the environmental conditions (Hillman, 1987).

The mean home range described for females and young (222 km^2, but it may be up to 425 km^2), is largest than for any other African species of large ungulate, with the exception of elephant (*Loxodonta africana*). Mean home range described for males is around 50 km^2. They do not defend an area from other males. The disparity between male and female home-range size is also an unusual feature in the antelopes (Hillman, 1988).

In the Lokop Dam Nature Reserve, the association patterns between adults (females and males) follow an annual cycle centred on the breeding season (November-January; Fig.2). During the calving season (August-October) the group size increases due to association between females and young, and at the same time males associated together. After the calving season almost all females and young are in the same herd, and males are absent. From November till January the nursery group included some males. During this period bull groups behave more aggressively while the nursery herd is more peaceful. From February to April, when the calves were weaned, small mixed groups leave and rejoin the nursery herd. The mixed

age/sex groups tend to become more homogeneous during May to September (Underwood, 1975).

Figure 2. Annual cycle of the variations in the group composition of common eland in South Africa. Relative size of the groups is show by the size of the circles. Calves are indicated as CC. 1) Yearlings and subadults join to the small nursery groups. Over the calving season the groups merge, but bull associations can be seen separated from the females. 2) After the peak of calving, most of the young and females stay in the same herd (nursery group). From October to January 2 to 6 adult bulls may join the females herd. Only-bull groups show a peak of aggressiveness in this period. 3) At this time small mixed sex/age groups spilt from the main herd. 4) The small mixed sex/age groups become more homogeneous and the nursery herd consist mainly of young animals (and will be the basis of the next year nursery group). [This figure is adapted from Underwood (1975) and Groves *et al.* (2011).
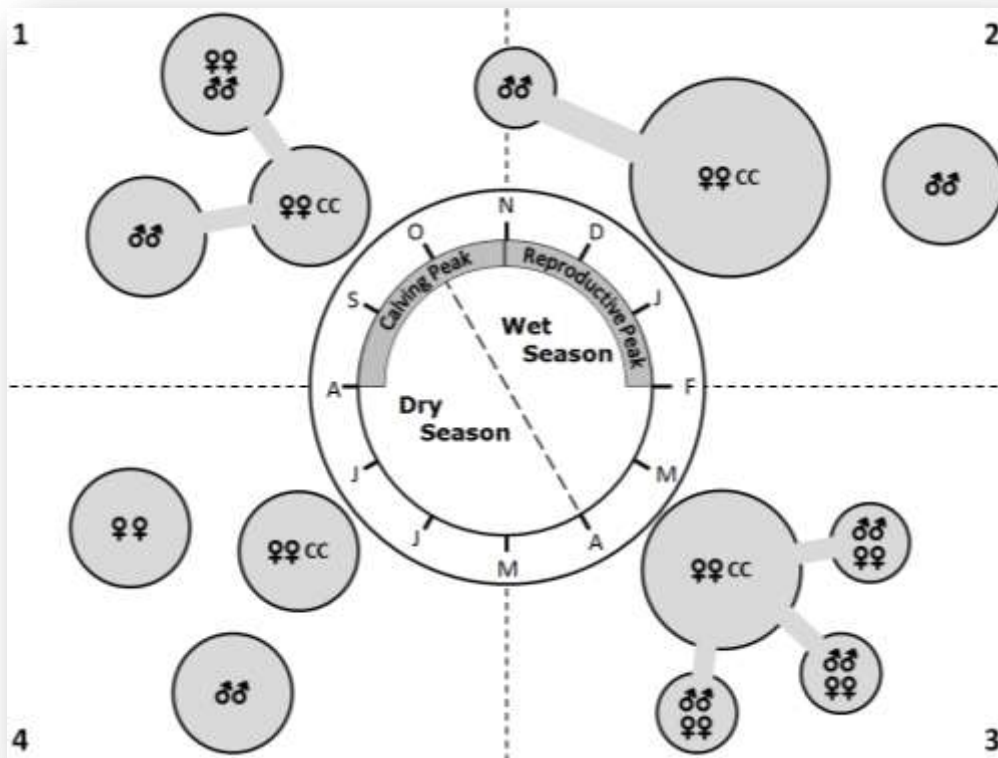
Low level of aggregation between males is observed during the winter (dry season). This low level rapidly increases during the pre-rut period, when bulls begin to show an increase in aggressive activities and tend to be found in pure bull groups. Female association is lower

during the parturition peak (August, September) presumably because the parturition cows look for isolation, and during the weaning period of the calves (February, March) when the females can move more freely of their calves and leave the nursery groups for days (Underwood, 1975).

1.3. BEHAVIOUR; SOCIAL AND AGONISTIC INTERACTIONS IN COMMON ELAND.

Eland communicate through visual displays, olfactory cues, and auditory signals (Pappas, 2002), and they have a well developed repertoire of visual signals (Kiley-Worthington, 1977).

The visual displays of common eland can be classified in four categories; 1. Postural movements, 2. Protective movements, 3. Orientation movements, and 4. Movements related to cutaneous irritation (Kiley-Worthington, 1977; also for the rest of the section).

As common eland hold an important amount of visual signals the research was mainly focused on postural and protective movements, which are the displays related with dominance/aggressive behaviours.

In postural movements, an increase in the postural tonus is marked by an increase in the elevation of the head and the tail (Fig. 3), and such postures are used in situations demanding attention, signalling "excitement". These movements send messages related to warning, and are often associated with aggressive approach. Lowered postural tonus, marked by a lowering of the head in synchrony with the tail, are associated with sick, sleepy or fearful animals and therefore are used by non-confident animals and subordinates.

Figure 3. Changes in postural tonus with increase in excitement (extracted from Kiley-Worthington, 1977).
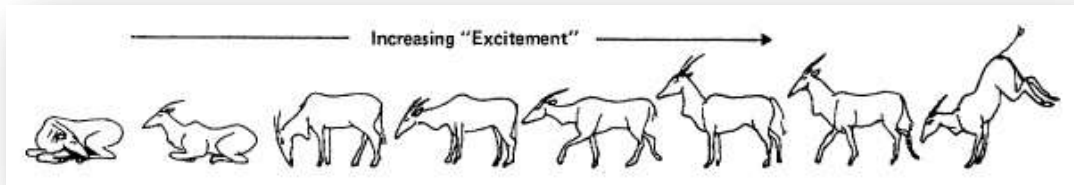
Protective movements, includes the movements and postures related to the horns, and thus include actions related to threat. These are head lowering, horn pointing, horn clashing, and wrestling, in increasing intensity.

In fights between male eland, horn wrestling and attempts to twist the neck are prolonged and potentially very dangerous. The thick muscular neck appears to be functional to avoid fight injuries, although the visual enhancement of the neck by a dewlap may have display function. In eland, the primary function of horns is as a weapon for use against predators and also conspecifics. Elands are horned from within a few weeks of birth in both sexes, and the horns are very effective as weapons even in the sub-adult animals. Adult elands can kill small predators and severely wound large ones. The horns are used in intraspecific fights, but their use is not highly ritualized as in some horned antelopes and threat movements are confined to obvious intention movements to strike. The horns are indeed used in rutting fights between males, but are used (especially by the females with young) predominantly for defence against predators and conspecifics for which they are very effective. The sexual dimorphism of the horns reflects this: the females have longer thinner horns ideal for delivering quick stabs, but not for the

characteristic horn wrestling of the males, whose horns are shorter and thicker. This wrestling is facilitated by the tremendous muscular development of the neck and shoulders. The spiral twists of the horns have been suggested to help guiding the head down and bind the horns together to make the fight less dangerous. Elands seem to lack ritualization in the fight. Nevertheless, fierce fights do not occur very often. This may be related to the fact that these animals do not defend territories in a strict sense, and frequently tolerate more than one male in the group, even during the rut.

Other movement where horns are involved is horn pointing, consists of a slight lowering of the head accompanied by the drawing in of the chin, so that the horns are pointed in the direction of the adversary, a failure to respond by the recipient may result in aggression. It can be described, therefore, as an intention movement to yield and is interpreted as a strong threat.

The horns in eland are also used for other activities such as breaking branches for browsing, and scratching. Horning the ground is a behaviour which occurs in many ungulate species, it is usually considered to be a threat. But this does not explain either why both animals should do it during confrontations, or why it is frequently performed in wild animals (waterbuck, eland and blesbok and various cervids), when no animals are around to see it. Where cutaneous glands are present on the head, it is possible that it may be used for scent marking. It is frequent to observe elands horning the ground and the fences, and the scent marking theory seems to explain more adequately this behaviour (personal observation). Other protective responses where horns are not involved are the withdrawal of the tail when protecting the rear, for example when an animal is chased.

The third type of movements, are the ones related to orientation, include visual responses and movements of the head and eyes in a particular direction. The function of such a display is to help other animals to locate potential sources of danger. Head turning towards the flank is a display common in oestrous females, directed at the male approaching the rear. Another head movement recorded, particularly in approach/avoidance situations, was a turning of the head away. This is often performed by the male when approaching a non-receptive female, and threatened by her. This action may represent a shift of attention reducing the conflict and allowing him to stay in the same place.

About the cutaneous irritation movements, it has been shown that activities related to this signals such as groom and head shaking have been incorporated into displays. Head rubbing on the ground can also be placed in cutaneous irritation category. In the females the head rubbing is confined to the period just before and after parturition. If it is the deposition of smell on the forehead that is the function of such behaviour, then it is possible that this could aid individual recognition, and calf-mother recognition thereby helping to cement mother-young bonds rapidly.

To conclude, eland present little evidences of ritualization in their displays, except for movements by males during preparation for mounting, and during the pronounced and static horn pointing, which shows some exaggeration.

1.4. COMMON ELAND DOMESTICATION

Eland is frequently considered to posses high potential for "domestication" and utilization by man as meat producer. The advantages quoted are the large size of the animal, the palatability of the meat, it's docility in captivity and it's being a browser of "marginal" cattle country. The social organization and seasonal movements of the species have been unknown or ignored, but have considerable bearing in its potential (Hillman, 1987). In East and South Africa were several attempts to domesticate common eland in first half of 20th century (Posselt, 1963; Skinner, 1967; Roth, 1970; Retief, 1971; Lightfoot 1977; Carles *et al.*, 1981).

Eland was reported to be handled like cattle in a pen (Bothma, 1996). However, the most sustained effort in the domestication of eland have been done outside of Africa in Askanya Nova, Ukraine, where elands have been successfully bred since 1892 (Treus and Lobanov, 1971). They were kept under similar conditions to those of domestic livestock (Treus and Kravchenko, 1968; Treus, 1983). The first practical experiences about farm breeding of common eland in the Czech Republic were reported by Hrouz (1995). Nowadays, common eland is recommended for the domestication by FAO (Scherf, 2000).

1.5. DOMINANCE AND AGGRESSIVE BEHAVIOUR IN UNGULATES

Several gregarious mammals are organized in stable and linear social hierarchies (Thompson, 1993; van Noordwijk & van Schaik, 1999; Côté, 2000; Veiberg *et al.,* 2004), some examples are ring-tailed lemur (*Lemur catta*; Norscia and Palagi, 2015), spotted hyena

(*Crocuta crocuta*; Holekamp *et al.*, 1996) and guanaco (*Lama guanicoe;* Correa *et al.*, 2013). The establishment of dominance relationships between individuals usually involves the use of aggressive behaviours, which can be modulated by the value of the contested resource and by changes in body condition of individuals (Appleby, 1980; Rutberg, 1986; van Schaik, 1989; Grenier *et al.,* 1999; Taillon and Côté, 2007). Many social mammals, however, exhibit fission–fusion societies (Aureli *et al.*, 2008; Haydon *et al.*, 2008), *e.g*., some bats (Kerth and König, 1999), dolphins (Connor *et al.,* 2007), elephants (Wittemyer *et al.*, 2005), where social bonds often appear to be ephemeral and are challenging to quantify. Nevertheless, these possibly subtle and dynamic social behaviours can create intricate networks of relationships (Croft *et al.*, 2011).

In animal societies individuals often engage in aggressive interactions with each other. When winners and losers are easily identified, such interactions are usually referred to as dominante–subordinate interactions. Based on who wins against whom, all or most individuals can be ranked in a dominance hierarchy (Bang *et al.*, 2010). Many dominance hierarchies observed in nature have been found to be completely or nearly linear (Chase *et al.*, 2002; Chase and Seitz, 2011). Linearity in this context means that the top ranking individual dominates all other individuals, the one with second-highest rank dominates all individuals besides the top ranker and so on, with the lowest-ranking individual being dominated by (*i.e.*, subordinate to) all others (Schmid and de Vries, 2013). An alternative measure for analyzing the linearity of a group structure is the triangle of transitivity. The triangle transitivity and linearity are essentially equivalent when dominance relations of all dyads are known, although they differ in that the triangle of transitivity is based in the dominance relationships among sets of three players that all interact with each other (Shizuka and McDonald, 2012).

In ungulates, competitive interactions can be divided into those in which opponents aggressively engage with each other but do not make physical contact (non contact interactions) and fighting that usually involves contestants locking horns or antlers and engaging in a vigorous pushing contest (Jennings and Gammell, 2013). Common types of noncontact interaction include vocalisation contests (Clutton-Brock and Albon, 1979), displacement interactions; horn or antler displays (Alvarez, 1993; Jennings *et al.,* 2002) and parallel walks (Clutton-Brock and Albon, 1979; Jennings *et al.,* 2003). Similar to noncontact interactions, fights also contain a variety of distinct actions such as the jump clash, charge, slam, butt and push (Geist, 1971; Clutton-Brock and Albon, 1979; Mloszewski, 1983; Estes, 1991; Alvarez, 1993). It is generally known that males communicate their strength, dominance or aggressiveness via horn/antler displays.

Evidence that antler or horn displays serve to convey individual quality during contests, independent of factors such as age or body size, has remained somewhat elusive (Vanpé *et al.*, 2010). Moreover, although the length of the structure is often related to dominance (Jennings *et al.,* 2006), the contention that these structures serve to reduce fighting by facilitating assessment (Geist, 1966, 1991; Lincoln, 1972) has received only limited support (*e.g.*, Wahlström, 1994, Jennings *et al.,* 2006). Fighting represents the most intense competitive phase of ungulate contests involving repeated clashing of the antlers and horns The body mass of mature males, in combination with their weaponry means that intraspecific fighting is dangerous and occasionally lethal (*e.g.*, Geist, 1971; Wilkenson and Shank, 1976; Clutton-Brock *et al*., 1979; Poole, 1989). Factors affecting the fight structure in ungulates are weapon size, body weight, opponent's familiarity, value of the contested resource and the form of assessment process (Jennings and Gammell, 2013).

Aggression serves a great variety of social functions, and it is hard to find any part of the social life of bovid where aggression is not involved (Walther, 1984; Rajagopal *et al.*, 2010). Also aggression has shown to be a powerful mechanism for intra-sexual and natural selection among males leading to sexual dimorphism in the size and shape of the horns and body proportions (Lundrigan 1996; Perez-Barberia *et al.*, 2002; Bro-Jorgensen, 2007; Wronski *et al.*, 2010).

Some studies divided aggressive interactions into (i) aggressive displays that included all agonistic displays with no physical contact; and (ii) fights which included any form of physical agonistic contact (Walther *et al.*, 1983, Blanka and Yanga, 2014), while others assessed aggressions by horn display, horns contest, and push (Cassinello and Pieters, 2000) threat, horn threat, rush threat (quick movement toward an opponent), and orientation threat (a low-intensity form of rush threat involving walking (Côté, 2000) evade, run away, displace, chase, rush, horn contact, horn clash, and intentional jump, mount performed toward males (Willisch and Neuhaus, 2010). Kiley-Worthington (1977) working with common eland as well, measured dominance by threats and fights and withdraws, and distinguish fights from play fights.

Seems to not be an agreement when it comes to assess dominance/aggressiveness displays, however distinguish between contact and non contact interactions is generally used.

2. RESEARCH AIMS

- To assess the behavioural characteristic among different age and sex group classes according to social displays.
- To quantify the linearity of the groups by two methods.
- To evaluate if the indexes of quality of the linearity are different for different group structures, and if they differ according to the kind of interactions recorded.

As different group structures has been reported in the wild [multi male groups, females with calves in nursery groups and mixed groups (Underwood, 1975; Hillman, 1987, 1988)], we expect different social behaviour and uses of the displays among the groups, and the existence of linear dominance hierarchies in the different group structures, as has been show in previous research with bovid (Cransac and Aulagnier, 1996; Wirtu *et al.*, 2004; Sárová *et al.*, 2013). Moreover, the existence of differences in the strength of the linearity among the different social groups is probable due to differential social behaviour and differential uses of the dominance and/or aggressive displays in the studied groups.

3. MATERIALS AND METHODS

3.1. DATA COLLECTION

The study was conducted in the CULS farm in Lány (Czech Republic) starting with a herd of 35 individuals of *T. o. pattersonianus* (18 females, 12 males and 5 calves) in February 2014 to 40 individuals (18 females, 7 males and 15 calves) in January 2015. The installations are divided in an enclosed stable with two corridors and two open pastures of 2 ha.

For the data collection "sampling all occurrences of some behaviours" method was chosen due to (i) observational conditions are excellent, (ii) the behaviours are sufficiently "attention-attracting" that all cases will be observed, and (iii) the behavioural events never occur too frequently to record (Altmann, 1974). The behaviours recorded were group into three categories; (1) Dominance, (2) Aggressive and (3) Affiliative. Aggressive behaviour was consider when there was a direct contact between individuals in a dominance display; therefore pushing, yielding and wrestling were consider under this category. Dominance behaviour includes the aggressive behaviour (contact displays) plus threatening, and passing, the non contact dominance displays. Grooming, mounting and playing among young were included in affiliative behaviour.

Animals were identified by ear-tags and natural marks as horn shape and pelage coloration also help the identification. During the observations binoculars Canon 10X30 IS we used when needed.

The observations were conducted approximately every second week since February 20014 to January 2015 with a total of 7,719 interactions observed in seven different group types (different social structures) during 170 hours. The animals were, according to the weather conditions, inside the stable or in the pastures. Within the same herd seven different groups were observed during the study period; calves, females and calves, females with calves and a single male, females with a single male, mixed groups of males and females, mixed group including calves, and males. In total, 32 groups were studied (Table 1).

Table 1. Sex/age composition of the groups observed in this study. In order to improve the analyses, the observations were joined in general group structures mainly based on the dominant sex in the group.

Observed groups	n	Group Structures	n
Females+Calves	9		
Females+Calves+Male	5	Females	15
Females+Male	1		
Mixed	5	Mixed	9
Mixed+Calves	4		
Males	7	Males	7
Calves	1	Calves	1
TOTAL	32		

The groups can be considered as independent observations, since small changes among them happened continuously during the observation period due to farm management reasons and new born calves. For statistical reasons, the initial group structures were rearranged into super groups (dominated by females, males, mixed groups and calves) in order to increases the number of observations and obtain more robust results.

3.2. ANALYSIS OF THE GROUP STRUCTURE

In order to assess the structural characteristics of the groups, it was determined the strength of the dominance hierarchy in the studied groups by two different methods: Linearity (h') and transitivity ($tTri$).

3.2.1. Linearity and transitivity

In order to know, understand and assess the dominance hierarchy of a social group, the first step should be to know the linearity of the group. For this reason, the linearity of the studied groups was analyzed by two different methods.

Linearity was measured by de Vries (1995) extension of Landau's (1951) linearity index h'. Landau's index uses counts of dominations to infer the degree of linearity in an interaction matrix. Landau's h might be biased by gaps in the data. An unbiased estimate of h (h') was devised by de Vries together with a procedure that statistically tests whether the assumption of linearity h' is statistically supported (Schmid and de Vries 2013). A value of 1 indicates complete linearity and a value of 0 indicates that each individual dominates an equal number of other individuals (de Vries, 1998). A strictly linear hierarchy is one in which higher ranked individuals dominate all individuals of lower rank. Within a strictly linear hierarchy, all dyads have a dominant-subordinate relationship. The triangle transitivity and the linearity are essentially equivalent when dominance relations of all dyads are known, although they differ in that the triangle transitivity is based in the dominance relationships among sets of three players that all interact with each other (Shizuka and McDonald,

2012). Dominance relations for every set of three players (triads) are 'transitive': when individual A dominates B and B dominates C, then A also dominates C (Chase, 1982; de Vries, 1995). Complete observations where all dyads are known are rare in empirical studies, therefore the triangle of transitivity has two major advantages: it does not require 'filling in' of unobserved relations, and its expected value is constant across group sizes. Shizuka (2012) defined the triangle transitivity (*tTri*) as a scaled index of the relative frequency of transitive triads among all the triangles (closed triads) in a dominance network, the value of tTri ranges from -3 (the relations are cyclical) to 1 (the relations are transitive).

Both analyses were performed in the software DomiCal (Schmid and de Vries, 2013). Linearity test (*h'*) was executed with 10.000 randomizations and the triangle transitivity (*tTri*) test with 1.000 randomizations.

3.2.2. Statistical analysis

IBM SPSS statistic 20 was the software used for the statistical analyses. Behavioural and linearity data was tested for normality, and according to Kolmogorov-Smirnov test all the variables followed a normal distribution, with the exception of wrestling behaviour in dominance and aggressive analyses. Those variables following a normal distribution were analyzed using parametric statistic (ANOVA, Post-hoc Tukey-test, paired Student t-test, and Pearson correlation). Non parametric statistic (Kruskal-Wallis) was used for the not normal variables.

4. RESULTS

4.1. CHARACTERIZATION OF THE BEHAVIOURS USED IN DIFFERENT GROUP STRUCTURES

In a first step, the existence of differences among the studied group structures for the relative occurrence of affiliative and aggressive behaviours was analyzed, and individually for each studied display (Table 2). The group that only counts with one observation (calves) was excluded from the analysis.

Table 2. Studied displays and their categorization.

Display	Category
Groom	
Play	Affiliative
Mount	
Threat	Dominance
Pass	
Wrestle	Dominance
Push	+
Yield	Aggressive

4.1.1. Relative occurrence of non-affiliative interactions

The occurrence of non-affiliative interactions, understood as the percentage of dominance interactions in a group compared with all the observed interactions (affiliative + non-affiliative), showed absence of differences for the studied groups (ANOVA: n=31, $F_{(2,30)}$=1.032, p=0.369; Table 3). Post-hoc Tukey-test also showed

lack of differences between single groups, *i.e.*, all the studied groups showed similar relative occurrence non-affiliative behaviours.

Table 3. Mean and standard deviation of the studied non-affiliative behaviours in the different group structures, and ANOVA test result for differences among the groups. Post-hoc Tukey-test also showed lack of differences between single groups.

Group	n	Mean±SE	F	p
Females	15	0.9112±0.0238		
Mixed	9	0.9559±0.0128	1,0321	0,3694
Males	7	0.9246±0.0232		
Calves	1	0.8647		

The occurrence of non-affiliative behaviours was homogeneous among the groups, being those much more frequent that the affiliative behaviours in all the studied groups. Calves showed highest performance of affiliative displays.

### 4.1.2. Relative occurrence of aggressive interactions

Table 4. Mean and standard deviation of the studied aggressive behaviours in the different group structures, and ANOVA test results for differences among the groups. Post-hoc Tukey-test also showed lack of differences between single groups.

Group	n	Mean±SE	F	p
Females	15	0.3884±0.0398		
Mixed	9	0.3447±0.0376	2.797	0.078
Males	7	0.5389±0.0944		
Calves	1	0.6641		

The occurrence of aggressive interactions, measured as the percentage of aggressive interactions compared with the total of dominance behaviours observed (see Table 4), showed not significant differences among the groups (ANOVA: n=31, $F_{(2,30)}$=2.797, p=0.078; Table 4). Post-hoc Turkey-test also pointed out the homogeneity of the groups.

Nevertheless, this difference is on the edge of significance. Groups dominated by males seem to perform more aggressive behaviours than groups dominated by females and mixed groups. The higher occurrence of aggressive displays observed for calves, in contrast to the value observed for affiliative interactions, suggests that their relations are either affiliative or aggressive.

Figure 4. Mean and standard deviation of Non aggressive interactions (pass, threat) *vs.* Aggressive interactions (push, yield, wrestle) in the studied group structures.
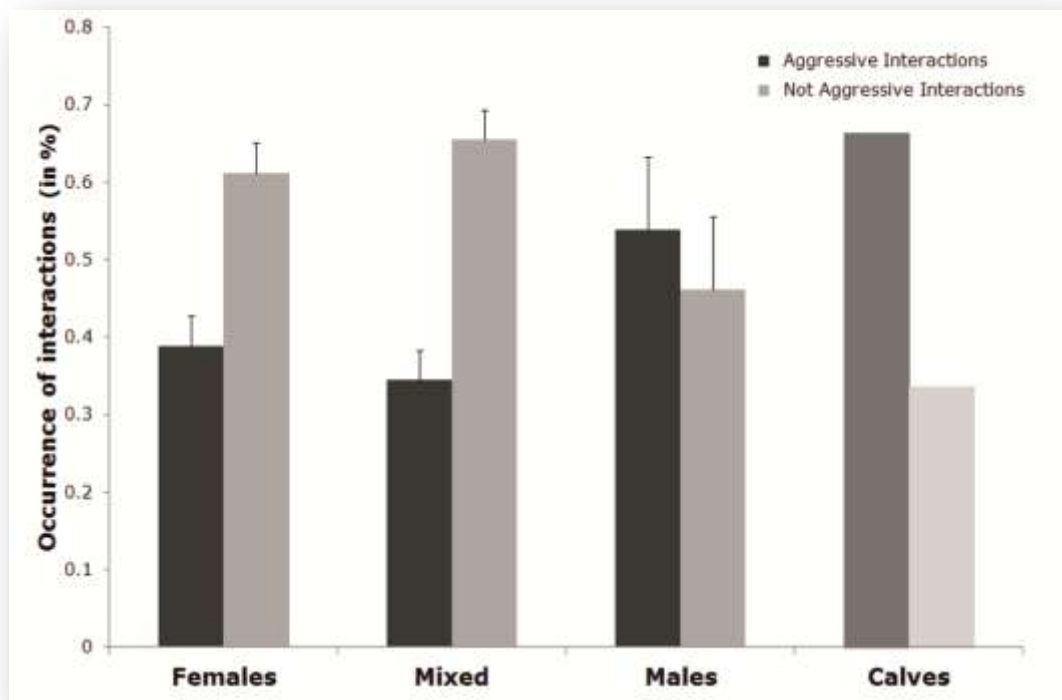
Student's t-test shows a significant difference in female (n=15, t=-2.802, p=0.014) and mixed group (n=9, t=-4.126, p=0.003) displays of dominance, being the non contact behaviours the most commonly used. While male groups do not present differences in the uses of contact and non contact dominance displays, aggressive displays are more often performed (Fig. 4).

4.1.3. Relative occurrence of dominant displays

Table 5. Mean and standard deviation of dominance displays in the groups, and ANOVA/ Kruskal-Wallis results for differences among the group uses of the displays plus Post-hoc Tukey-test results.

Group	Females n=15	Mixed n=9	Males n=7	Calves n=1	F	p
Push ± SE	**0.2219 ±0.0470 ab**	**0.1066 ±0.0175 b**	**0.3189 ±0.1063 a**	0.3817	2.643	0.089
Yield ±SE	0.1630 ±0.0195	0.1755 ±0.0138	0.1310 ±0.0305	0.2672	0.863	0.433
Wrestle ±SE	**0.0035 ±0.0013 b**	**0.0626 ±0.0289 a**	**0.0890 ±0.0281 a**	0.0153	6.195	**0.006**
Threat ± SE	0.2347 ±0.0273	0.3187 ±0.0509	0.2024 ±0.0533	0.0992	1.792	0.190
Pass ±SE	0.4224 ±0.0371	0.3366 ±0.0610	0.3454 ±0.0807	0.2366	0.881	0.425

SE=standard deviation.
Groups detected in the post-hoc Tukey-test are indicated as superscript.
In bold are highlighted the significant values for the ANOVA / Kruskal-Wallis tests.

The occurrence of the five kinds of dominance interactions studied (push, yield, wrestle, threat and pass) in the studied groups are shown in Table 5. The most performed display in all groups is pass, and the lest is wrestle. The occurrence of dominance displays in the groups indicated wrestling as the only behaviour that differs among them (Kruskal-Wallis: n=31, $U_{(2,30)}$=17.600, p<0.001). Pushing, although is not significant, is a marginal value (ANOVA: n=31,

$F_{(2,30)}=2.643$, p=0.089) and Post-hoc Tukey-test analysis shows the biggest differences between males and mixed group for pushing behaviour. Males and mixed perform more wrestling than females while males perform more push than mixed groups.

4.1.4. Relative occurrence of aggressive displays

Aggressive behaviours understand as dominance displays that involves physical contact are push, yield and wrestle. The difference occurrence of this displays are showed in Table 6. Push is the display more performed by females and males groups, while yield is more use by the mix groups. Wrestle and yield are use differently by the age/sex groups (for Wrestle, Kruskal-Wallis: n=31, $U_{(2,30)}=16.711$, p<0.001; for yield, ANOVA: n=31, $F_{(2,30)}=3.296$, p=0.052). Post-hoc Turkey-test indicated that mixed and females groups perform more yield display than males. Kruskal-Wallis tests showed that females use significantly less wrestling than mixed and male group, being wrestling more often performed by male groups.

Table 6. Mean and standard deviation of aggressive displays in the groups, and ANOVA/ Kruskal-Wallis results for differences among the group uses of the displays plus Post-hoc Tukey-test results.

Group	Females n=15	Mixed n=9	Males n=7	Calves n=1	F	p
Push ± SE	0.5252 ±0.0570	0.3207 ±0.0571	0.5288 ±0.1090	0.5747	2.676	0.087
Yield ±SE	**0.4658** **±0.0560** [a]	**0.5386** **±0.0577** [a]	**0.2913** **±0.0630** [b]	0.4023	3.296	**0.052**
Wrestle ±SE	**0.0091** **±0.0035** [b]	**0.1407** **±0.0531** [a]	**0.1798** **±0.0601** [a]	0.0230	6.948	**0.004**

SE=standard deviation.
Groups detected in the post-hoc Tukey-test are indicated as superscript.
In bold are highlighted the significant values for the ANOVA / Kruskal-Wallis tests.

4.2. LINEARITY STUDY OF THE GROUPS

4.2.1. Landau's linearity index (h')

The Landau´s linearity index showed a significant positive correlation with the number of interactions collected during the study. Both for dominance (Pearson correlation: n=32, r= 0.734, p<0.001; Fig. 5) and aggressive interactions (Pearson correlation: n=32, r=0.790, p<0.001; Fig. 6) h' increases when the number of interactions per dyad increases.

Significance for the value of h' was achieved with around 0.75 interactions observed per dyad both for dominant (Fig. 7) and aggressive (Fig. 8) behaviours. Nevertheless, the significance level was frequently not achieved because of the lower number of aggressive interactions collected.

The 3 points with higher p h' value correspond from higher to lower to females plus calves, mix group with calves and females plus calves.

Figure 5. Landau's *h'* values correlated with the number of interactions per dyad in the dominance behaviours of all observed groups.
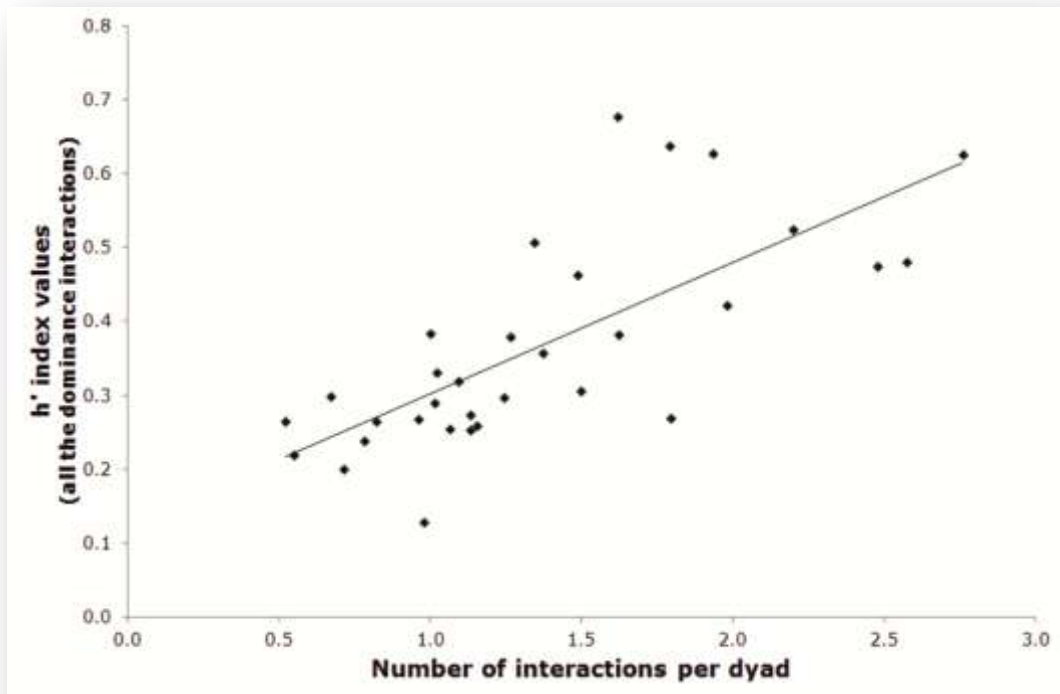
Figure 6. Landau's *h'* values correlated with the number of interactions per dyad in the aggressive behaviours of all observed groups.
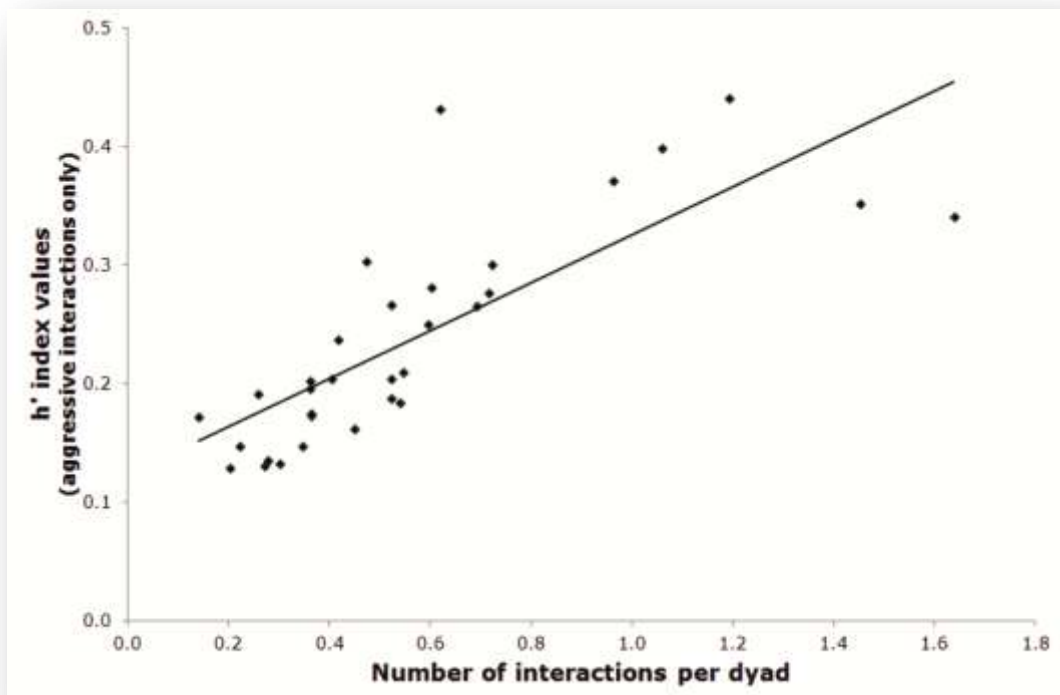
Figure 7. Significance values for *h′* in dominance behaviours for all observations correlated with the number of interaction per dyad.
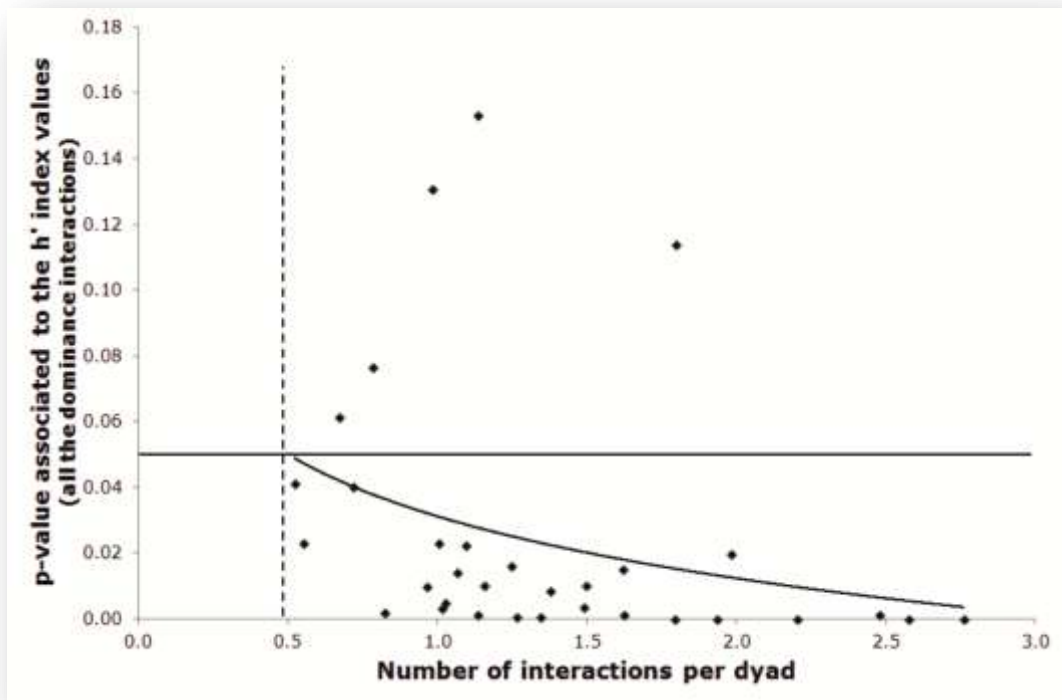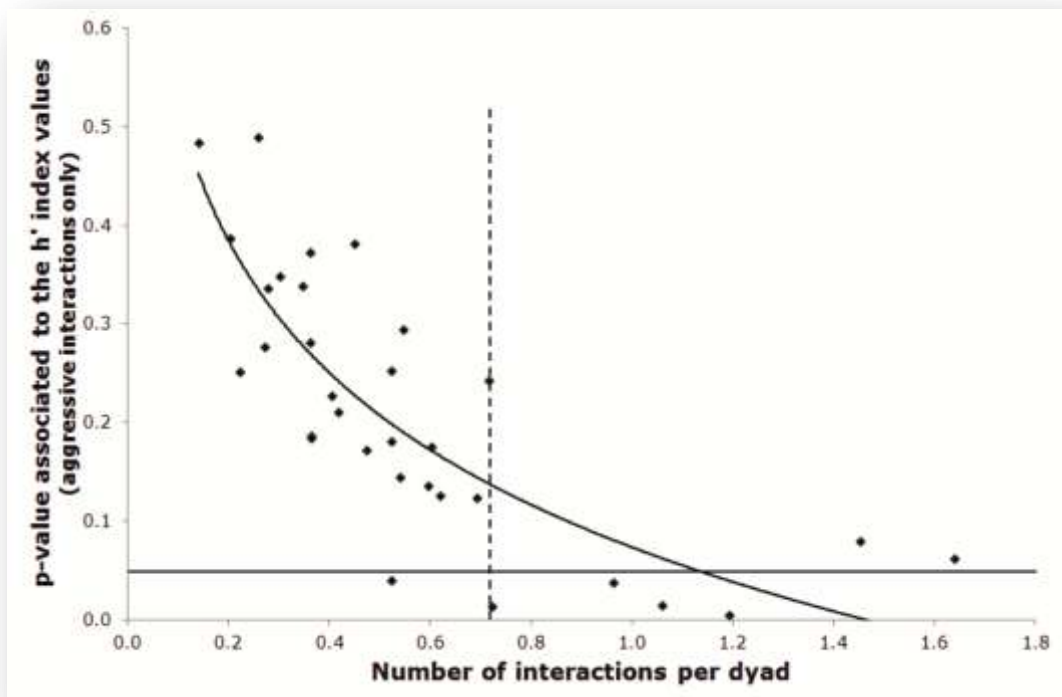

Figure 8. Significance values for *h′* in aggressive behaviours for all observations correlated with the number of interaction per dyad.

4.2.2. Triangle transitivity (*tTri*)

Values of *tTri* show a positive correlation with the number of interactions for dominance (Pearson correlation: n=32, r=-0,359, p=0.044; Fig. 9) and for aggressive interactions (Pearson correlation: n=32, r=-0.469, p=0.007; Fig. 10). When we compared the values of *tTri*, this appears to be more stable regardless the number of interactions in dominance interactions, with a small trend to decrease *tTri* value when the number of interactions per dyad increases in aggressive interactions.

A significant value of *tTri* required 0.5 interactions per dyad and significant results were more often obtain for aggressive (Fig. 12) interactions than in *h'* (due to the lower number of interaction required), also transitivity values were always significant for dominance interactions (Fig. 11).

Figure 9. Triangle transitivity values for all dominance interactions observed in the groups correlated with the number of dyad.
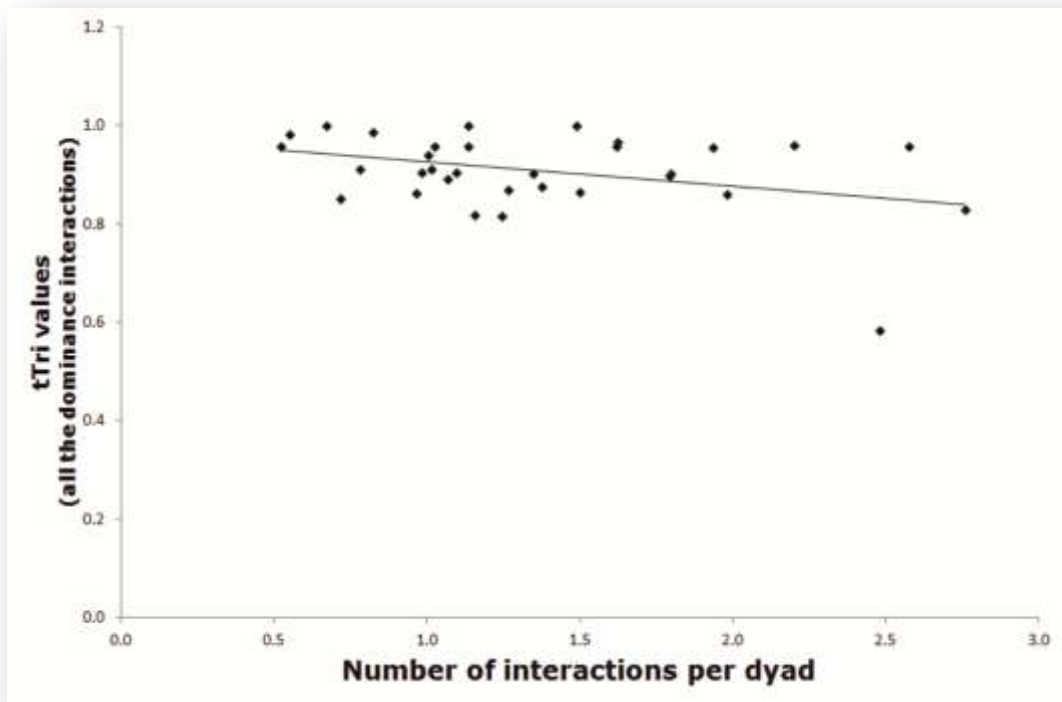

Figure 10. Triangle transitivity values for all aggressive interactions observed in the groups correlated with the number of dyad.
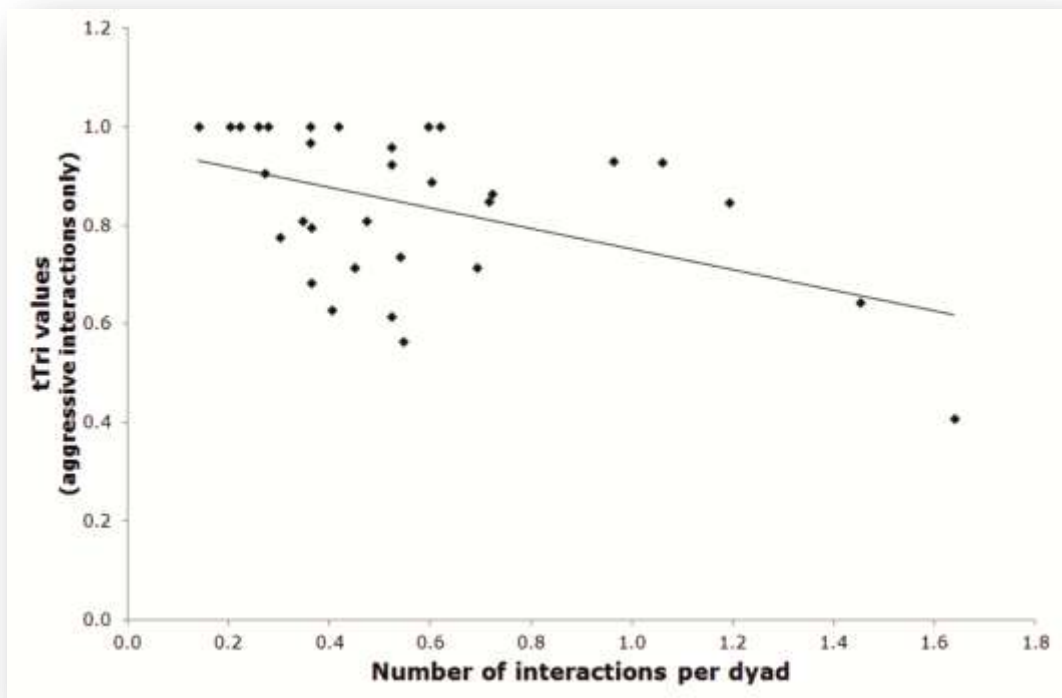
Figure 11. Significance values for *tTri* in dominance behaviours for all observations correlated with the number of interaction per dyad.
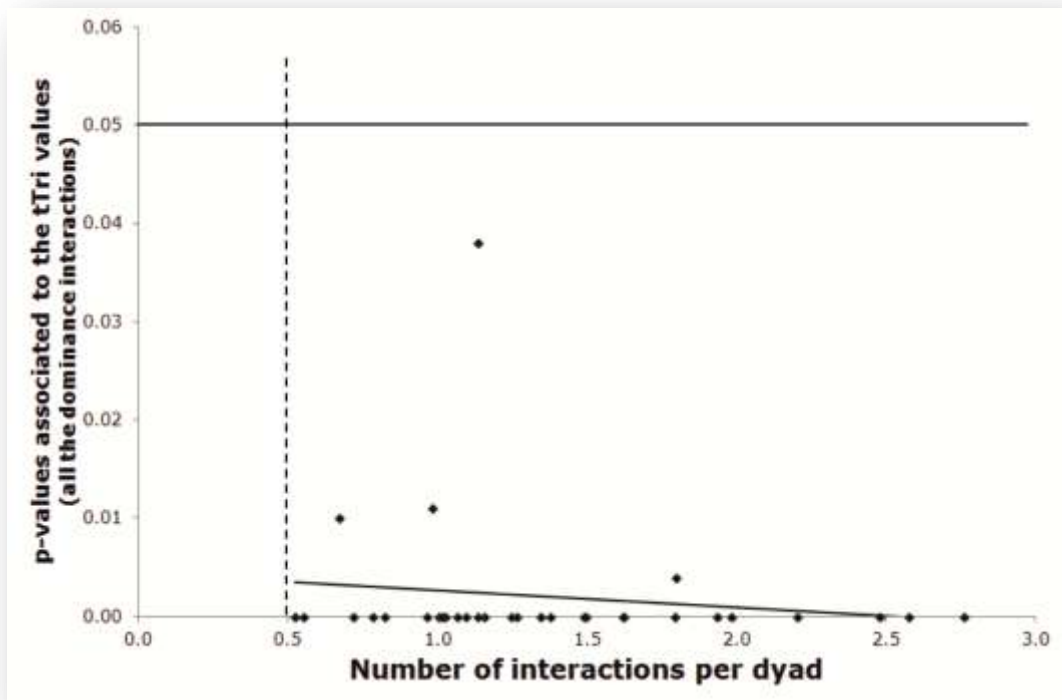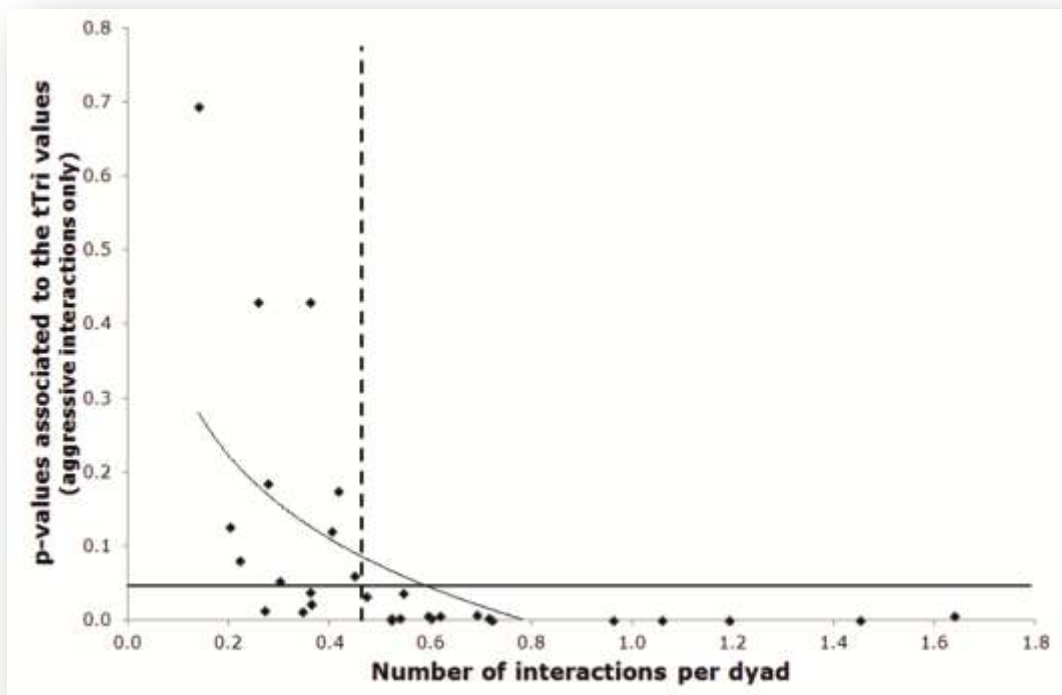

Figure 12. Significance values for *tTri* in aggressive behaviours for all observations correlated with the number of interaction per dyad.

4.2.3. Differences in linearity among group structures

Landau's linearity values for dominance behaviours showed statistical differences among the groups (ANOVA: n=31, $F_{(2,30)}$=3.590, p=0.041; Fig. 13). Post-hoc Turkey-test showed higher linearity in the males group respect the females and mixed groups.

Figure 13. Mean and standard deviation of dominance behaviours linearity values of Landau *h'* for the studied groups and Post-hoc Tukey-test results.
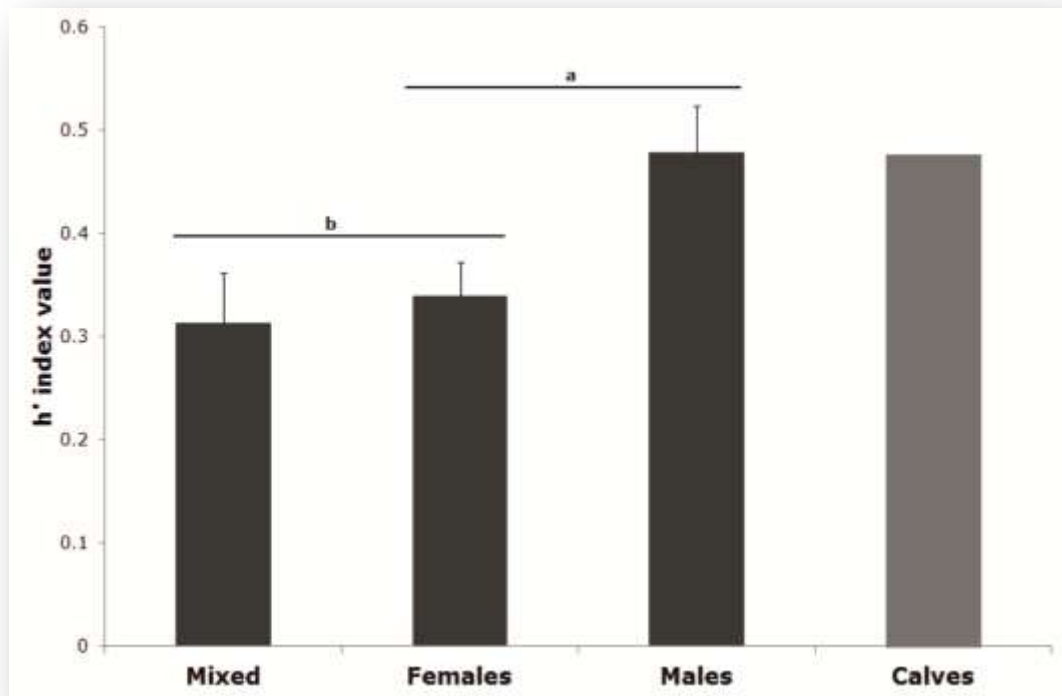

The same analysis was made for *tTri* data and non significance differences were found among the groups.

4.2.4. Proportions of decided dyad

A decided dyad is when dominance behaviour was observed in only one of the two individuals (Schmid and de Vries, 2013). The proportions of decided dyad (Fig. 14) shows a normal distribution according Kolmogorov-Smirnov test, and the ANOVA analysis shows significant differences among the groups (ANOVA: n=31, $F_{(2,30)}$=5.626; p=0.009) Post-hoc Tukey-test indicates that the males groups have a higher proportion of decided dyad than females and mixed groups, that show a similar, and lower, proportion of decided dyad.

Figure 14. Mean and standard deviation of number of decided dyad in the groups in dominance interactions and Post-hoc Tukey-test results.
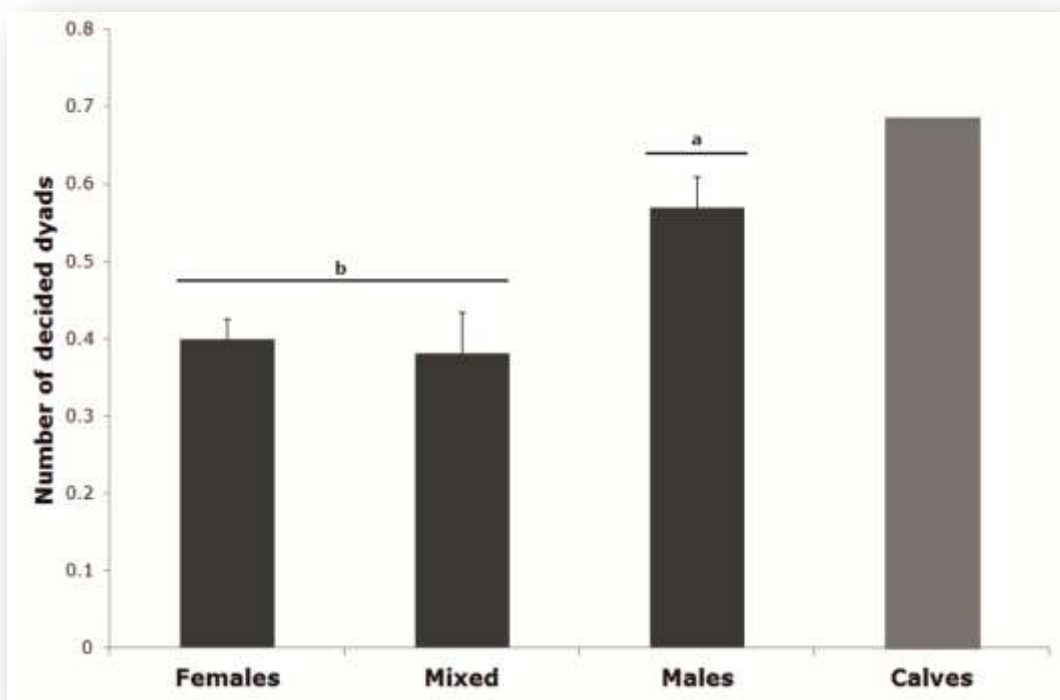
5. DISCUSSION

The results highlight that different group structures in the common eland [based on females, males or mixed groups, which are the main group structures found in the wild for this species (Underwood, 1975; Hillman, 1987)] have clear differences in the use of different behavioural interactions among individuals. These differences also lead to the existence of differences in the strength of the linearity (for Landau's index *h'*) of the social hierarchies in each studied group structure (summarized in Table 7). Male-based groups are more aggressive, wrestle more, and show marked up linearity. Female and mixed based groups are more peaceful, aggressive displays occur less often, and present lower values of linearity. The aggressive display more often seen amongst female-based groups is yielding, while they show lower frequency of use of wrestling than mixed or male-based groups.

Table 7. Summary of the results obtained in this study. Main performed behaviours and Landau's linearity index strength is shown for each studied social structure.

Group Structure	Frequent social behaviours	Linearity
Females	Non-contact dominance displays. High occurrence of yield.	Low linearity
Mixed	Non-contact dominance displays. High occurrence of yield and wrestle.	Low linearity
Males	Equal use of contact and non-contact dominance displays. High occurrence of wrestling.	High linearity
Calves	High occurrence of aggressive and affiliative behaviours.	High linearity

Within the linearity methods, results show that Landau's linearity index is a more accurate estimator for two reasons: it is less permissive (requires a higher number of observations to provide a significant value), and it offers more behavioural information about the group structure (it is possible to identify differences in linearity among groups).

5.1. CHARACTERIZATION OF THE SOCIAL INTERACTIONS AMONG DIFFERENT GROUP STRUCTURES

No significant differences were found among the studied groups for the relative occurrence of affiliative and non affiliative displays. Non affiliative behaviours are much more common, consistently higher than 85% of the social interactions recorded among the various research groups. Calves are the group structure displaying a higher frequency of affiliative behaviour (14%) while mixed group displayed the lowest (4%).

The occurrence of contact (aggressive) *vs.* non contact agonistic displays was also not significant, *i.e.*, all groups use the aggressive displays in a similar way. Nevertheless, females and mixed groups show a parallel trend in the use of non contact behaviours, which are used more than the aggressive ones. Among the male-based groups, contact and non contact behaviours are used similarly, with contact displays just slightly more frequent. It is interesting that the proportion of aggressive interactions within the calves group is the highest among the observed groups (even if just one observation was made). They perform mostly affiliative behaviours and aggressive ones, with low proportion of non contact behaviours. The high occurrence of affiliative behaviour may be linked with the fact that

young and calves are the ones who show long-lasting relationships while they are in the nursery groups (Hillman, 1987). The preference for aggressive displays over non contact ones can be understood as practice for serious contests in the adulthood, but also as a mechanism for the early establishment of hierarchy among the young which may be based in weight in animals in the same age class (See Sárová *et al*., 2013 for similar results in cattle).

Thus, non affiliative behaviours seems to be very important for every kind of herd, which agrees with the importance of aggressive behaviours in bovids social system found previously in other studies (Rajagopal *et al*., 2010). Although the different group structures use aggressive displays similarly, female-based groups are more peaceful than bulls groups, which behave more aggressively (Underwood, 1975). The predominant use of non contact displays in females was also seen in adult cows, which do not always use physical strength to show dominance (Sárová *et al*., 2013). It is known that dominance can be influenced by factors such age and body mass (Arnott and Elwood, 2009; Sárová *et al.*, 2013), and thus, further analysis of the data obtained for each individual in the frame of this project will provide a better explanation, even though no relationship between dominance and weight and age was found in previous studies in captive female elands (Wirtu *et al*., 2004).

The analysis of each individual agonistic display (*i.e.*, both contact and non contact interactions) showed differences in the use of push and wrestle. Pass and threat are used similarly for all the studied group structures, being pass the most performed dominance display. Male based groups use push displays significantly more than mixed groups, while female-based groups use wrestle less often than mixed

and male-based groups. Nevertheless, no differences in the use of non contact agonistic displays were observed among the groups.

When only the contact interactions were analysed, it was highlighted that yield has a higher occurrence in females groups whereas wrestle was more used by males groups. This can be related to the sexual dimorphism of the horns: females have straight long horns ideal to stab, while male horn shape is adapted to wrestle (Kiley-Worthington, 1997). Mixed groups keep some intermediate pattern of displays, performing yield more than male-based groups, and wrestle more than female-based groups. This intermediate performance (between the values observed for male- and female-based groups) found in several results for the mixed groups, suggests that these mixed groups are not in fact united social structures, but just the relaxed temporary joining of two certainly united sex-based social structures. Results about the linearity of the different group structures also support this idea (see the following section). Further analyses of these groups using different techniques (like using other software for the determination of social matrices, like SocProg) may also help to prove this hypothesis.

5.2. LINEARITY, TRIANGLE TRANSITIVITY AND RELATION WITH SOCIAL BEHAVIOUR

The definition of dominance has been based on the confrontation of individuals in agonistic interactions (Norscia and Palagi, 2015). Previous research on ungulates about hierarchy focused on creating the dominance rank among individuals based on dominance-aggressive displays (Cransac and Aulagnier, 1996; Cassinello and Pieters, 2000; Berg, 2008; Willisch and Neuhaus, 2010). A linearity

structure in these researches can be inferred for the hierarchy ranking data, but linearity measures is rarely calculated and when it does it received little attention.

Landau's index (h') and triangle transitivity ($tTri$) tested for dominance and aggressive social interactions indicated that in all the studied groups (with an adequate amount of data collected) the dyadic interactions are linear and the triadic interactions are transitive. Therefore the evidence claims that all the studied herd structures have a linear hierarchical structure (See Wirtu *et al*., 2004 for similar results).

A deep analysis of both indexes (h' and $tTri$) showed differences between them. Values of $tTri$ and h' are correlated with the number of interactions per dyad (*i.e.*, the amount of observed interactions). However Landau's index needs at least 0.75 interactions per dyad to provide a significant linearity, while $tTri$ needs only 0.45 interactions per dyad to provide significant transitivity.

Datasets of dominance behaviours were always larger (reaching up to 3 interactions per dyad) than datasets for aggressive behaviours (were a maximum of 1.8 interactions per dyad were obtained); the significant value for aggressive interactions in h' and $tTri$ test was rarely achieved therefore any conclusion can be made until farther observations are obtained, but based on the different use of dominance and aggressive displays by sex based groups, differences in the linearity among group structures for aggressive behaviours are expected, as there were found for dominance linearity values. Norscia and Palagi (2015) uses Landau's index and triangle transitivity to

assess the social structure of different groups in lemurs based on aggressive and avoidance behaviours.

Differences among the groups were tested based on *h'* and *tTri* for dominant behaviours. It was found that *tTri* do not provide any farther information about the sociality of the groups, since all the studied groups show similar values of transitivity, *i.e.*, they have a linear structure but all the groups have the same strength. Nevertheless, the values of *h'* showed significant differences among the studied group structures: male-based groups have a significantly higher linearity female-based and mixed group.

The differences found in linearity between groups can be related with the group structure function. In the wild, aggressive behaviours increase in bull groups and most of the fights take place during reproduction season (Underwood, 1975), this can be related with the establishment of a hierarchy for the access to females. A similar pattern has been found in American bison (*Bison bison*) by Wolff (1998). A strong hierarchy in male groups have biological sense as can be directly linked with the accesses to females and reproductive success since, in polygynous mammals, mating success of males often depends on intense male-male competition (Wolff, 1998; Mainguy *et al.*, 2008).

The higher linearity found in male-based groups is also supported by the fact that more decided dyads were observed than in mixed and female-based groups reflecting that the dyadic relationships are more clearly established in male-based groups.

The differences between significant values correlated with the number of observations in the indexes (Landau's index requires higher number of interactions), sum to the lack of differences among groups for *tTri*, point out that Landau's linearity index as a more accurate method to assess linearity in social ungulates and it also provided more information about the groups behaviour.

6. CONCLUSIONS

In a herd of 40 common eland, and based on 7,719 observations collected during 170 hours from February 2014 to January 2015, it is demonstrated that different group structures have clear differences in the use of behavioural interactions. These differences also lead to the existence of differences in the strength of Landau's linearity index of the social hierarchies: males show a stronger hierarchy than females and mixed groups.

Dominance behaviours were the most common among the studied groups; females and mixed groups use more non contact displays than males which behave more aggressively. The differential use of displays may be linked with the way the social hierarchy is built and it seems to differ among the group types.

The differences in aggressive displays can be related with the sexual dimorphism of the horns; female horns are adapted to stab, and they performed more yielding than males. Male horns are adapted to fight and they perform more wrestle than females.

Both Landau's index (*h′*) and triangle transitivity (*tTri*) highlighted that the studied groups show a linear social structure. Within the linearity methods Landau's linearity index is more accurate for two reasons: it requires a higher number of observations to provide a significant value and it offers behavioural information about the group structure.

Further investigations are needed to clarify the hypothesis that mixed groups are not in fact united social structures, and to clarify the function of aggressive behaviours among calves: if it is related to the early development of hierarchies or to leaning for future contests. Future studies should focus in understanding the behaviour in other complex social structures in common eland. The study of the hierarchy and social structure among different group types with attention to the specific displays can lead to determine the basis of dominance in the species and improve the data collection in the wild populations.

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8. Index of Tables and Figures

FIGURES

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