Czech University of Life Sciences Prague

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Maternal Behaviour in Giraffes

(Giraffa camelopardalis)

PhD Thesis

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ALLONURSING IN CAPTIVE GIRAFFES

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STATEMENT

I declare that I prepared this dissertation thesis entitled "Maternal behaviour in Giraffes (*Girafa camelopardalis)* " alone and that I used the literature that is mentioned in the references. All presented photographs were taken by myself.

In Prague: 2.9. 2016 Markéta Gloneková

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ABSTRACT

Allomaternal care is one of the most interesting types of cooperation among females. Its most extreme form is allonursing, nursing of a non-filial young, which is still not completely understood, even though many hypotheses have been postulated. This type of cooperation among giraffes had not been expected for long time. This was based on the initial opinion that giraffes do not have social system and form only weak social bonds. However, my bachelor and master theses showed high occurrence of allonursing in captive giraffes.

The first aim (1) of this thesis was to test all possible hypotheses explaining allonursing in captive giraffes. However, a lot of the information needed to test them were missing, which resulted in the formulation of further aims. The second aim (2) was to test the hierarchy in captive giraffes. The third aim (3) was to describe the growth and weight of captive giraffes. The fourth aim (4) was to compare nursing patterns in the zoo and in the nature reserve Bandia, Senegal and the last aim (5) was to test the social bonds among giraffes in the nature reserve Bandia, Senegal.

(1) From 2007 - 2011, the nursing behaviour of 24 females and 37 calves was observed. Eighty-three percent of the females allonursed a nonfilial calf and 86.5% of calves allosuckled from a nonmaternal female. Allonursing in giraffes was explained by milk-theft from the point of view of the calves and possible reciprocity among females. (2) The agonistic interactions of 31 giraffes were recorded in four herds. A linear hierarchy was been found among giraffes and rank was significantly affected by age and time spent in the herd. (3) The weight data from 43 giraffes in Prague zoo were collected from 2009 - 2013 and provided the basic information about giraffe growth and weight. (4) I also observed the nursing behaviour of seven and four female-calf pairs in the fenced Bandia reserve, Senegal, and in Prague zoo, respectively, both for 22 days. The differences in nursing patterns were likely to reflect anti-predator behaviour, the population density of animals and the distribution of food resources. (5) Finally, I investigated the social preferences of 28 introduced giraffes in semi-captivity in the nature reserve Bandia, Senegal and provided the results supporting the existence of a fission-fusion social system among giraffes with social preferences among adult females.

The overall results provide unique findings on allonursing in general as well as changing our perspective on giraffe social behaviour.

Key Words: Maternal behaviour, allonursing, social behaviour, hierarchy, weight, growth, giraffe, *Giraffa camelopardalis*

ABSTRAKT

Alomateřská péče je jedním z nejzajímavějších typů spolupráce mezi samicemi. Extrémní formou alomateřské péče je alokojení, kojení nevlastního mláděte, které stále není jednoznačně pochopeno, ačkoliv k jeho vysvětlení byla stanovena řada hypotéz. Tuto formu spolupráce mezi žirafami nikdo nepředpokládal, neboť se dlouho předpokládalo, že žirafy nemají rozvinutý sociální systém a tvoří pouze velmi slabé sociální vazby. Výsledky mojí bakalářské a diplomové práce však ukázaly vysoký výskyt alokojení u žiraf v zoologické zahradě.

Prvním cílem (1) této práce bylo testovat všechny hopotézy, které by mohly vysvětlovat alokojení u žiraf v zoologické zahradě. Mnoho informací potřebných k naplnění prvního cíle ale chybělo, proto vznikly cíle další. Druhým cílem (2) bylo testovat hierarchii žiraf v zoologické zahradě, třetím (3) popsat růst a hmotnost žiraf v zoologické zahradě, čtvrtý cíl byl (4) porovnat kojení v zoologické zahradě a v přírodní rezervaci Bandia v Senegalu a poslední cíl (5) testovat sociální vztahy mezi žirafami v přírodní rezervaci Bandia v Senegalu.

(1) V letech 2007 – 2011 bylo sledováno kojení 24 samic a 37 mláďat. Osmdesát tři procent samic alokojilo nevlastní mláďata a 86.5% mláďat alosálo od cizích samic. Alokojení bylo vysvětleno pomocí hypotézy krádeže mléka z pohledu mláďat a reciprocitou z pohledu samic. (2) Byly sledovány agonistické intereakce 31 žiraf ve 4 stádech a prokázána lineární hierarchie. Postavení žiraf v rámci této hierarchie bylo signifikantně ovlivněno věkem a dobou strávenou ve stádě. (3) V letech 2009 – 2013 byla sbírána data o hmotnosti 43 žiraf v pražské zoo, tyto údaje daly vznik prvnímu přehledu o žirafím růstu a hmotnosti vůbec. (4) Pozorovala jsem také kojení 7 a 4 dvojic samice-mládě v přírodní rezervaci Bandia v Senegalu a v Zoo Praha, obě skupiny po dobu 22 dní. Byly nalezeny rozdíly v kojení způsobené pravděpodobně antipredačním chováním, hustotou populace a distribucí potravních zdrojů. (5) Nakonec jsem také zkoumala sociální preference 28 introdukovaných žiraf v přírodní rezervaci Bandia v Senegalu. Výsledky podporují existenci sociálního systému fission – fusion a sociálních preferencí mezi samicemi žiraf.

Všechny závěry této práce jsou velmi unikátní a přinášejí jak nové výsledky o alokojení obecně, tak mění původní pohled na sociální chování žiraf, které bylo několik let opomíjené.

Klíčová slova: Mateřské chování, alokojení, sociální chování, hierarchie, hmotnost, růst, žirafa, *Giraffa camelopardalis*

1. CONTENT

1. INTRODUCTION

Cooperation is currently a very attractive topic in behavioural ecology (Clutton-Brock 2009; Bshary & Oliveira 2015; Engelhardt 2016). An especially important form of cooperation is common parental care or allomaternal care (Clutton-Brock 1991; Engelhardt 2016), since raising young requires a great deal of energy (Sadleir 1984; Clutton-Brock 1991; Gittleman & Thompson 1988). An extreme form of allomaternal behaviour is allonursing (Cameron et al., 1999a), a phenomenon where a female nurses young or young ones that are not her own (Packer et al. 1992; Roulin 2002). This behaviour is still not understood, even if it is found in many mammalian species and many hypotheses exist, as different studies obtained different results and came to different conclusions (Boness 1990; Cassinello 1999; Nunez et al. 2013; Zapata et al. 2009b; Zapata et al. 2010; Maniscalco et al. 2007; Brandlová et al. 2013; Víchová & Bartoš 2005; Engelhardt et al. 2015).

When I started this research, giraffes (*Giraffa camelopardalis*) were thought to be animals without a social system and social bonds (Estes 1991). Moreover, some studies indicated that the relationship between mother and young giraffe is weak (Dagg & Foster 1976), because calves spent more time with other young than with their mothers (Saito 2009). Contradicting this opinion is the fact that giraffes create so-called "nurseries" (*crèches*), groups of young guarded by one female (Pratt & Anderson 1979). The creation of nurseries could be understood as a form of common parental care (Riedman 1982). Despite this fact, giraffe social behaviour has not been studied for many years.

Recent studies, including this thesis, produced the opposite results and confirm the existence of a social system as well as a stronger bond between the mother and calf than was previously argued (Bercovitch et al. 2006; Bercovitch & Berry 2010; Carter et al. 2013b). This thesis is the result of long-term research started in 2007 by observing the nursing behaviour of giraffes in Prague zoo, which I joined in 2008 and which provided the first results in the form of my bachelor and master's thesis. I discovered an extremely high rate of allonursing in captive giraffes, which represents more than 50% of all nursing. Such a rate remains one of the highest occurrences in mammals and makes the giraffe a very suitable species for studying allomaternal behaviour.

The main aim was to test all the possible hypotheses explaining allonursing. However, a lot of information needed to test the hypotheses was missing – the existence of a hierarchy in giraffe females in the zoo was unknown, social bonds among the females both in the zoo and in the reserve needed to be clarified and information about the weight and growth of giraffes in general has not been published before. For this reason my first aim to study allonursing changed somewhat and I have been trying to fill in the gaps in the story of giraffes through my other aims. Therefore, the final form of this thesis consists of four articles and one manuscript (submitted after major revision). All of them relate to the maternal and social behaviour of giraffes, mostly in the zoo, partly in a nature reserve in Senegal.

I believe that my thesis helps to understand both allonursing behaviour in general and the related behaviour of the giraffe, an animal who everyone knows, but still holds many surprises.

2. THEORETICAL BACKGROUND

2.1. Maternal behaviour

Parental care in general is the strategy which helps offspring to survive, thereby increasing the fitness of a parent’s offspring (Clutton-Brock, 1991) and enhancing the parents' reproductive success (Klopfer 1967; Trivers 1972). The parental care evolved by natural selection and its origins lies at the basis of social behaviour (Darwin 1871). There is a great diversity of parental care patterns (Clutton-Brock 1991; Krebs & Davies 2012): biparental care when both parents care, uniparental care when only the male or only female cares or no care. Some species exhibit multiple patterns of care, where more than one of these basic patterns is present (Clutton-Brock 1991; Webb et al. 1999). There are few, if any species of mammal, and certainly no species of ungulate, in which the young can survive in the absence of maternal care (Alexander 1988) as the nursing relationship between the young and the mother is the most important (Gubbernick 2013).

The maternal-filial relationship has been considered a special relationship and very intensive in ungulates (Klopfer 1967). Among ungulates, two strategies are known; offspring follow the mother (‘‘following’’ strategy) versus species in which the offspring remain hidden (‘‘hiding’’ strategy; Fisher et al. 2002). These two strategies also differ in their nursing behaviour. While shorter and more frequent suckling bouts occur in followers, the nursing of hiders takes place only a few times per day but is longer (Carl & Robbins 1988).

2.1.1. Allomaternal behaviour

Allomaternal behaviour is the behaviour devoted to a non-filial young and is most common in cooperative breeding societies (Solomon & French 1997). However, allomaternal care is very costly in terms of the mother's energy (Maniscalco et al. 2007; Trivers 1974). Over 120 mammalian species were reported to be cooperative breeders (Riedman 1982). Cooperative breeding could be explained as breeding females' assistance in the protection and feeding of other females' offspring (Lukas & Clutton-Brock 2012). Animals that are active in taking care of other family members are called “helpers” (Krebs & Davies 1981). Franck (1996) and also Krebs and Davies (1981) prefaced that helpers are often not related or are only a distant relation (Clutton-Brock 2002). So-called allomaternal behavior has been reported in many groups across mammalian orders and includes various degrees of common care (Riedman 1982). Common nesting (Komdeur 1994), babysitting a group of young from different females by only one female (Doolan & Macdonald 1999), the creation of "nurseries" (*creches*) formed of the young ones of different females (Bon & Campan 1996) where each female becomes a babysitter in turn (Riedman 1982; Stanford 1992). Nurseries relieve females from various maternal activities, especially from nursing (Riedman 1982).

2.1.2. Allonursing

Allonursing or allosuckling is suckling behaviour between a female and a non-filial offspring of the same species (Packer et al. 1992). The term allonursing is used when a female nurses a non-filial calf and allosuckling when a calf suckles from a non-maternal female (Bartoš et al. 2001ab; Drábková et al. 2008; Zapata et al. 2009ab). Packer et al. (1992) created the pivotal list of species as he assambled data on more than 100 species of mammals. Allonursing has been reported in almost 70 taxa in his study. Packer's work was a very important launching point for research into allonursing. Many of his sources were on the basis of personal communication and many have been not published yet. Appendix 1 shows the allonursing species reported from Packer's research, contains both the original and current sources and has grown to more than 100 allonursing species.

Allonursing is not yet completely understood, because lactation is very energy-demanding (Gittleman & Thompson 1988) and the risk of transmission of pathogens between the female and the non-filial calf is increased (Roulin 2002). On the other hand, allosuckling is easier to understand, as the young ones can gain more energy supply, compensate for growth deficiency (Bartoš et al. 2001a) or get a more diverse spectrum of immunoglobulins, if they suckle from several females (Roulin & Heeb 1999). The causes of alloparental care may be based on endocrinological levels of prolactin, future direct fitness, present and future indirect fitness, and social structures providing opportunities for the expression of parent-like behaviour in an alloparental context (Mumme 1997). Many hypotheses explaining allonursing which are not mutually exclusive have been formulated.

2.1.2.1. Kin selection hypothesis

The kin selection hypothesis suggests cooperation among relatives (Clutton-Brock 2002). The female nurses a non-filial calf only if they share genes (Packer et al. 1992). More precisely, this hypothesis predicts that females preferentially nurse more or less related than unrelated offspring. A review of empirical evidence for this prediction requires a distinction between species in which social groups are often composed of closely related females (Hayes 2000) or of a mixture of related and unrelated individuals (Roulin 2002). Several studies supported the kin-selection hypothesis as a possible explanation for allonursing in ungulates (Ekvall 1998; Engelhardt et al. 2016b).

2.1.2.2. Reciprocity hypothesis

The reciprocity hypothesis suggests cooperation among individuals of the same herd (Roulin 2002). This hypothesis assumes that one animal helps another (allonurse the non-filial offspring) and expects that the recipient will help back (Roulin 2002). According to Pusey & Packer (1994), two females raise young of a higher fitness when they nurse each other's offspring than when they do not share milk. The benefits for a female of having her offspring nursed by other females should be so large that she agrees to reciprocate by nursing the offspring of others to ensure that members of her group will continue to nurse her offspring (Roulin 2002). Usually, some individuals performed more allonursing than others (Murphey et al. 1991; 1995; Pusey & Packer 1994; Plesner Jensen et al. 1999). Reciprocating females may differ in their state of health and therefore if they exchange the same amount of similar quality milk, they may pay a different cost of doing so (Roulin 2002). Only two recent studies supported reciprocity as an explanation for allonursing in ungulates (Engelhardt et al. 2015; Jones & Treanor 2008) and a few other studies did not exclude reciprocity as a possible explanation of allonursing (Ekvall 1998).

2.1.2.3. Parenting hypothesis

In the parenting hypothesis, the female improves her maternal skills (Packer et al. 1992; Roulin 2002). Therefore, this hypothesis suggests that the primiparous (and less experienced) females will allonurse more than the multiparous (thus more experienced) females (Roulin 2002). This hypothesis is particularly relevant in species in which young, virgin females lactate spontaneously, since in these species the females can acquire maternal skills without having to pay the cost of producing offspring. The parenting hypothesis is unlikely to apply to females that nurse alien offspring alongside their own. This is because the nursing of genetic offspring should be sufficient to gain maternal experience (Roulin 2002). Empirical evidence of this is still lacking.

2.1.2.4. The hypothesis of social benefits

In hierarchically ordered societies, adult females could also receive social benefits by allonursing non-filial calves. According to this hypothesis of social benefits, females preferentially allonurse the offspring of dominant females (Packer et al. 1992; Roulin 2002; Baldovino & Di Bitetti 2007). By nursing non-filial offspring females may have access to a social group, increase their social status or avoid aggression from conspecifics (Riedman 1982; Plesner Jensen et al. 1999; Roulin 2002). Packer et al. 1992 in his list of allonursing animals noted one case of a dominant female allonursing the young of a subordinate female. This information was obtained by personal communication and has never been confirmed or clarified in any research articles.

2.1.2.5. The milk evacuation hypothesis

Females can nurse non-filial offspring to evacuate the surplus milk that their own offspring do not consume (Wilkinson 1992). ‘Therefore, the milk evacuation hypothesis does not apply when a female nurses an alien offspring while her own offspring are still hungry and attempt to suckle foster mothers’ (Roulin 2002). Wilkinson (1992) proposed that well-fed females nurse allosucklers to evacuate the rest of their milk before resuming foraging activities. In this way, they may reduce their own body weight, avoid teat infection, and reduce painful pressure in the breast (Lee 1987; O’Brien & Robinson 1991). Allonursing as a strategy to evacuate milk may also explain females that lose their young and adopt other young (Riedman & Le Boeuf 1982), as it may enable females to lose body weight quicker (Roulin 2002).

2.1.2.6. The misdirected parental care hypothesis

In this case the female cannot recognize that she is nursing a non-filial calf, often found in young or primiparous unexperienced females (Roulin 2002; Zapata et al. 2009b; Maniscalco et al. 2007). This hypothesis can be included among the non-adaptive behaviour arising from unnatural conditions or high density of animals (Clutton-Brock & Harvey 1979) and would persist as a by-product of a group living where the benefits of breeding close to each other are greater than the costs, including those associated with allomaternal care (Pusey & Packer 1994; Manning et al. 1995). Furthermore, misdirected parental care is more common in animal groups producing larger litters, as it may be more difficult to find a non-filial offspring in the group of filial ones (Packer et al. 1992).

2.1.2.7. The milk theft hypothesis

The misdirected parental care hypothesis is often connected with the milk theft hypothesis (Roulin 2002; Brandlová et al. 2013), explaining the behaviour of the non-filial calves "stealing" the milk without the female noticing (Zapata et al. 2009b; Packer et al. 1992). Milk theft or “parasitism” is most widespread in monotocous taxa (Murphey et al. 1995; Packer et al. 1992). The calves mostly suckle in positions where it would be difficult to identify them (Zapata et al. 2009b) or together with the filial calf (Brandlová et al. 2013).

2.1.2.8. The compensation hypothesis

The compensation hypothesis suggests that offspring allosuckle to compensate for low birth mass, insufficient maternal milk supply or inadequate growth (Roulin & Heeb 1999; Víchová & Bartoš 2005). A few studies found that calves are probably allosucking to compensate for previous deficiencies in maternal milk (Zapata et al. 2010; Víchová & Bartoš 2005) which is in line with the compensation hypothesis.

2.1.2.9. The hypothesis of improved nutrition

The improved nutrition hypothesis states that offspring improve their nutrition, and hence mass gain, by the ingestion of non-maternal milk in addition to maternal milk

(Engelhardt et al. 2016a). The improved nutrition hypothesis was found in domesticated red deer, *Cervus elaphus* (Landete-Castillejos et al. 2005) and reindeer (*Rangifer tarandus*; Engelhardt et al. 2016a).

2.2. The Giraffe

2.2.1. Giraffe status, subspecies and numbers

Giraffe as a species *(Giraffa Camelopardalis)* is listed as Least Concern in the IUCN Red List as the species remains widespread, with a total population numbering more than 100,000 individuals. However, the population trend is declining. Some populations remain stable, but some are genuinely threatened (Fennessy & Brown 2010).

Giraffe subspecies classifications are still being investigated and changing (Dagg & Foster 1976; Kingdon 1997; East 1999; Grubb 2005; Groves & Grubb 2011), and have been confusing and even contradictory for nearly 250 years (Fennessy 2008). The taxonomic and even geographic limits for the subspecies remain uncertain (Fennessy & Brown 2010) and recent genetic work suggests that several subspecies could be reclassified as species (Brown et al. 2007). It is widely accepted that there are nine subspecies: *G. c. angolensis, G. c. giraffa, G. c. peralta, G. c. reticulata, G. c. rothschildi, G. c. tippelskirchi, G. c. antiquorum, G. c. reticulata and G. c. tippelskirchi* (Brown et al. 2007; Hassanin et al. 2007; Brenneman et al. 2009). Furthermore, there is Tornicroft's giraffe, *Giraffa camelopardalis thornicrofti*, which is a geographically isolated subspecies of giraffe found only in north-east Zambia (Fennessy et el. 2013). This subspecies seems to be the most closely related to the subspecies *G. c. tippelskirchi* (Fennessy et el. 2013).

There are two subspecies of giraffes whos status is "Endangered", *G. C. peralta* and *G. c. rothschildi*. *G. C. peralta* subspecies is a genetically unique population (Suraud et al. 2012). Their current population trend is increasing under targeted conservation programmes. This subspecies survives only in the wild (Hassanin et al. 2007) in a number fewer than 200 individuals (Fennessy & Brown 2010). Rothschild's current population is still decreasing. The estimates of the wild population are below 2,500 mature individuals. However, the numbers are declining overall and no subpopulation is estimated to contain more than 250 mature individuals. The population is potentially close to meeting the population threshold for "Critically Endangered" under criterion C (Fennessy & Brown 2010). According to the Zoological Information Management System (ZIMS) database, 578 individualRothschild giraffes currently live in zoological gardens.

Groves & Grubb (2011) divided the subspecies into the Northern complex which includes *Giraffa c. camelopardalis*; *Giraffa c. reticulata; Giraffa c. antiquorum*; *Giraffa c. peralta* and the Southern complex which include *Giraffa c. tippelskirchi*; *Giraffa c. thornicroft*; *Giraffa c. giraffa* and *Giraffa c. angolensis*. *G. c. rothschildi* and *G. c. camelopardalis* are synonymous in this study, but there is no morphological or genetic evidence to support this, therefore I still tend to classify the Rothschild giraffe as a subspecies, as does the IUCN Red List (Fennessy & Brown 2010).

2.2.2. Social behaviour of giraffes

Giraffe social behaviour has been neglected for many years. Giraffes live in groups whose composition is unstable and can change every day (Estes 1991), which is probably why these animals were described as forming only loose, unstable and frequently changing ties to their conspecifics (Estes 1991; Le Pendu et al. 2000). The only strong bond among giraffes was supported to be between a mother and her dependent calf (Langman 1977) and between young giraffes (Le Pendu et al. 2000). Many recent studies focused on giraffe social behaviour have been conducted that came to completely the opposite conclusions (Tarou et al. 2000; Bashaw et al. 2007; Bercovitch & Berry 2013a). Giraffe herds make a fission-fusion social system that is embedded in a larger community with a changing size and composition of herds (Bercovitch et al. 2006; Bercovitch & Berry 2010; Carter et al. 2013b; Bercovitch & Berry 2013b).

Giraffe females are more social than males. Males live in the herd until about three years of age and then form bachelors´ groups (Estes 1991). When they mature, they mostly become loners (Estes et al. 1991). In both cases they often merge with female herds (Estes 1991). The females compose the herds with other females and their calves. Most herds consist of a variety of age groups of both sexes (Bercovitch & Berry 2013b). Female giraffes showed a significant preference for, or avoidance of, other giraffes (Bercovitch & Berry 2013b) and therefore form a stable population of individuals that is divided into geographically distinct subgroups, despite the absence of physical barriers (van der Jeugd & Prins 2000; Carter et al. 2013b). Social ties in giraffe society could be influenced by kinship and social attraction, or may only associate because they have similar habitat preferences (Carter et al. 2013ab). The bonds among giraffes may persist through time (Bashaw et al. 2007).

A recent publication by Bashaw et al. (2007) demonstrated that captive giraffe females formed a complex social structure with strong relationships. Further, experimental social separation of captive giraffes proved the importance of social relationships to a specific individual (Tarou et al. 2000). Bashaw's other findings (2011) supported the fact that captive giraffes maintain strong relationships and suggested that studies of giraffe relationships were applicable across a range of captive conditions.

Giraffes are horned in both sexes and non-territorial (Estes 1991), with only adult males becoming territorial during the breeding season (Kingdon 2003). The dominance hierarchy has only been described for male giraffes (Coe 1967) and has not been deeply analysed. The theory that the long neck of the giraffe evolved to gain dominance in sexual encounters (Simmons & Scheepers 1996) is recently being abandoned (Mitchell et al. 2009, Wilkinson & Ruxton 2012). No studies dealing with the hierarchy of adult females have been made.

2.2.3. Maternal behaviour of giraffes

The relationships between giraffe mothers and their calves in early ontogeny are unclear. Giraffe calves have been described both as followers (Bercovitch et al. 2004) and as hiders (Langman 1977; Pratt & Anderson 1979). Ralls et al. (1986) claims that the calves exhibited a unique pattern. They were neither hiders nor followers. She ranked those giraffe as belonging to the "intermediate" cluster.

Before delivery, the female separates from the group to a hidden and inaccessible place (Estes 1991; Packer et al. 1992) and gives birth to her calf. After birth, the calf usually rises to its feet in 5 minutes (Kingdon 2003). During the first week, the calf spends half of the day lying down and is carefully guarded by the mother at night. They stay recluse for 1-3 weeks (Smithers 1983). Mother giraffes tend to form herds with other mothers. They seem to act in this way to protect their offspring from predation and they share responsibilities with other mothers (Bercovitch & Berry 2013b) in nurseries *(crèches;* Pratt & Anderson 1979; Horwich et al. 1983), specifically with offspring from about the 16th day of age (Pratt & Anderson 1979). Females spent most of the day looking for food or water, while leaving the group of young ones together (Pratt & Anderson 1979). One or more mothers are often nearby (Langman 1977; Horwich et al. 1983) but tend to leave the nursery of youngsters by themselves at midday (Kingdon 2003). Mothers come two to four times during the day to nurse the calf (Langman 1977) and return every evening before dusk to nurse the offspring and stay close to them all night (Estes et al. 1991). In captivity the social organization of herds also allows mothers to leave their calves in the safe environment of a *crèche*. They are tended by other giraffes, while the mother searches for food (Greene et al. 2006).

Juveniles begin to ruminate between their 3rd and 4th month; between the 12th and 16th month they are already fully separated (Estes 1991). They suckle up to the age of 13 months but remain associated with the mothers for another 2–5 months (Leuthold & Leuthold 1978). Social bonds between the mothers and calves persist past weaning until another calf is born (Langman 1977; Smithers 1983). Dagg (1976) characterized the bond between mother and her young giraffe as slightly weaker than what is known in other ungulates. The strongest bond between mother and calf exists for a year or one and a half years. Current studies indicate a stronger bond between the mother and calf than the previous ones (Bercovitch & Berry 2013b).

2.2.3.1. Nursing behaviour of giraffes

Nursing frequency has not been described in detail yet. However, the nursing frequency is highest in the first weeks after birth in the wild and also in captivity (Pratt & Anderson 1979; Horwich et al. 1983). The reported nursing duration in the wild is from 4 to 360s (Langman 1977; Pratt & Anderson 1979). Kaleta & Marczewska (2007) observed that nursing duration in the zoo is 120 – 360s. Nakamichi et al. (2015) observed nursing with a duration of approximately 60 s or less in captive giraffes when the young turned one month old. Giraffe calves of all ages in captivity and also in the wild attempted to suckle more often than the female allowed them (Pratt & Anderson 1979; Horwich et al. 1983).

2.2.3.2. Allonursing in giraffes

Allonursing in giraffes has not been studied before. Pratt & Anderson (1979) recorded several attempts to suckle from a non-maternal female in the wild. However, only one attempt was successful when a non-filial calf joined the filial nursing. No other cases of allosuckling in nature have been described since then. Kaleta & Marczewska (2007) observed that in captivity a non-filial calf suckled together with the filial offspring quite frequently. And also Dagg (1970) found that when the filial calf started to suckle, other calves and even adults came to join them.

3. AIMS OF THE THESIS

The main aim of this research was to describe the maternal behaviour of giraffes, with a special focus on nursing and allonursing behaviour in the zoo. To test all the possible hypotheses, I further aimed to observe the hierarchy among giraffes and perform a detailed analysis of giraffe weight and growth.

The next aim was to compare giraffe nursing behaviour in captivity and in the wild in the Bandia reserve in Senegal, with special focus on the modification of social behaviour under conditions of limited space. Further I aimed to test and confirm the presence of social bonds among herd members according to the association index.

4. MATERIAL AND METHODS

Descriptions of the methodologies are included in the particular articles in Results. Here I added useful information which could not be included in the articles due to their limited scope.

4.1. The observed animals

In the Prague herd, there was one male and six nursing female giraffes. One adult female died during the research. The number of young ones was changing during the observation period as new calves were born and a few older calves went to other zoos. One young female came to the herd. The number of calves present in the herd ranged from one to eight. Up to five young ones were one year of age (calves) and up to five were grownup juveniles (sub-adults). The herd composition is shown in Appendix 2, Table 1.

The herd of Olomouc zoo consisted of one adult male, four adult females, five sub-adult females and one sub-adult male. A sub-adult female was moved due to premature rut and one adult female came to the herd after delivery as her young one had died. The composition of the herd is shown in Appendix 2, Table 2. The composition of the herd in Liberec zoo did not change during the research and is shown in Appendix 2, Table 3. Also the composition of the herds in Dvůr Králové zoo was stable for the duration of the research period and is shown in Appendix 2, Table 4 and Table 5.

4.2. Management of stables of involved zoos

The management of the individual zoos was quite similar. The male remained in the herd for most of the observation period. The giraffes in Prague zoo were kept in a heated stable during most of the winter months, and moved to an adjoining yard during periods of maintenance. The herd spent most of their time in an outdoor enclosure on warmer days which was shared with common eland (*Taurotragus oryx spp*.), addax (*Adax nasomaculatus*), beisa oryx (*Oryx beisa*), red lechwe (*Kobus leche cafuensis*) and Grevy's zebra (*Equus grevyi*). The feed ration of giraffes from Prague zoo can be found in

Appendix 3, Table 1. Females in advanced stages of pregnancy or after parturition were additionally fed a milk mash.

In Olomouc zoo the stable occupied by animals for most of the winter was also heated. The giraffes went into a small outdoor enclosure with a solid concrete surface for a limited time according to the outdoor temperature. In the summer time, they were in a large grassy enclosure for most of the day. Chapman's zebra (*Equus quagga chapmanni*) can enter the giraffes' grassy enclosure. However, they have their own space inaccessible for giraffes. The feed ration of giraffes from Olomouc zoo is in Appendix 3, Table 2.

The animals in Dvůr Králové zoo had similar housing conditions, but when dwelling in the stable, the male was always separated and the herd split into females with calves and other animals. Their feed ration is given in Appendix 3, Table 3. In Liberec zoo, the giraffes spent most of the day outside in the summer (ca 10 hours) as well. In winter they went outside for at least one hour if the surface was not slippery. Their feed ration is given in Appendix 3, Table 4.

The zoo enclosures differed in size (Prague Zoo—400 m2 indoor, 2.2 ha outdoor, Liberec Zoo 700 m2 indoor, 0.1426 ha outdoor, Dvůr Králové Zoo—270 m2 indoor, 0.22 ha outdoor, Olomouc zoo— 150 m2 indoor, 360 m2 outdoor concrete paddock and 0.45 ha outdoor grassy paddock), but were similar in structure.

5. RESULTS

5.1. Stealing milk by young and reciprocal mothers: high incidence of allonursing in giraffes *(Giraffa Camelopardalis)*

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Stealing milk by young and reciprocal mothers: high incidence of allonursing in giraffes, *Giraffa camelopardalis*

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Allonursing, the nursing of nonfilial offspring, has been reported in a number of mammalian species; however, very few studies have investigated more than three hypotheses. The aim of our study was to investigate seven hypotheses explaining allonursing in captive giraffes. During 2007–2011, we observed 24 females and 37 calves in four zoological gardens in the Czech Republic, recording 2514 suckling events. We found that 83% of the females allonursed a nonfilial calf and 86.5% of calves allosuckled from a nonmaternal female; thus giraffes represent one of the highest occurrences of allonursing among non-domesticated mammals. The nonfilial calves more often allosuckled together with the filial ones than alone and tried to adopt positions where they may be harder to recognize, providing evidence for the milk theft hypothesis. In addition, the probability that a calf successfully allosuckled at least once from any female was higher when its mother allonursed successfully at least once than when she rejected calves. However, we found no evidence for the same rate of allonursing between reciprocal dyads of females and calves. Thus, we suggest that allonursing in giraffes is caused by offspring trying to steal milk and that females may tolerate this behaviour if reciprocal, in line with recent findings about giraffe sociality.

Lactation is the most costly parental investment for mammalian females, demanding more energy than gravidity (Clutton-Brock, 1991; Gittleman & Thompson, 1988). Therefore, allonursing, the nursing of nonfilial offspring, can be regarded as an extreme case of communal care (Pusey & Packer, 1994). Causes of alloparental care may be based on endocrinological levels of prolactin, future direct fitness, present and future indirect fitness, and social structures providing opportunities for the expression of parent-like behaviour in an alloparental context (Mumme, 1997). Allonursing may increase several risks, such as a lack of milk for the filial offspring and the high probability of pathogen transmission between females and the nonfilial offspring (Roulin, 2002).

Many hypotheses explaining allonursing which are not mutually exclusive have been formulated. These hypotheses explain allonursing either as an adaptive behaviour for females, or as an adaptive behaviour for the young, which may be nonadaptive for females (Emlen, 1982; Jamieson, 1989; Jamieson & Craig, 1987). Allonursing may have been favoured by reciprocal altruism (reciprocity hypothesis; Trivers, 1971), which predicts that females will reciprocate allonursing bouts provided to their respective infants. Reciprocal altruism has been documented in animal societies with elaborate social structures for behaviours where the costs paid by the donor are low in comparison with the benefits gained by the recipient (Davies, Krebs, & West, 2012). This reciprocal allonursing is hypothesized to occur when two females achieve a higher fitness when nursing each other's offspring to a similar extent than when they do not share milk (Pusey & Packer, 1994; Roulin, 2002), which could correspond with biological market theory (Noë & Hammerstein, 1994; Noë, Hooff, & Hammerstein, 2001).

The kin selection hypothesis (Hamilton, 1964) is one of the most frequent explanations of allonursing in societies composed of closely related females. It assumes that allonursing is preferentially directed to close kin and therefore serves to improve the inclusive fitness of the female. According to the parenting hypothesis, allonursing by inexperienced females may improve their ability to raise their own offspring (Packer, Lewis, & Pusey, 1992; Roulin, 2002), as has been documented for other allomaternal behaviours, for example spontaneous lactation (Creel & Rabenold, 1994). In addition, according to the milk evacuation hypothesis (Roulin, 2002),

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females can nurse nonfilial offspring to evacuate the surplus milk that their own offspring do not consume. ‘Therefore, the milk evacuation hypothesis does not apply when a female nurses an alien offspring while her own offspring are still hungry and attempt to suckle foster mothers’ (Roulin, 2002, p. 204). In hierarchically ordered societies, adult females could also receive social benefits by allonursing nonfilial calves. According to this hypothesis of social benefits, females preferentially allonurse the offspring of dominant females (Baldovino & Di Bitetti, 2007; Roulin, 2002).

Among nonadaptive hypotheses explaining allonursing from the female point of view, the misdirected care hypothesis is the most cited. According to this hypothesis, a female nurses a nonfilial offspring because she does not recognize that the offspring is not her own; in fact, the female is unable to discriminate her own offspring from a nonfilial one (Boness, 1990; Cassinello, 1999; Nuñez, Adelman, & Rubenstein, 2013). If allosuckling occurs due to misdirected care, the female does not reject the nonfilial young (Zapata, Gaete, Correa, González, & Ebensperger, 2009). Misdirected care is often found in young or primiparous inexperienced females (Maniscalco, Harris, Atkinson, & Parker, 2007) or in situations when the mechanisms for offspring recognition are violated (nest parasitism, high population density, captive conditions; Beecher, 1991). On the other hand, the female may be fooled by the nonfilial offspring's behaviour and nurse it alongside her own offspring without even noticing it.

Although the misdirected maternal care hypothesis is nonadaptive, the misdirected maternal behaviour may be explained by the adaptive milk theft hypothesis, when the offspring tries to steal the milk from a nonmaternal female by suckling in a specific position, for example, far from a female's head or behind the filial offspring (Packer et al., 1992). If the female recognizes that the calf is not her own, then she may refuse to nurse it (Brandlová, Bartoš, & Haberová, 2013; Roulin, 2002; Zapata, González, & Ebensperger, 2009). This behaviour has mainly been documented in high-density populations.

Young may suckle nonmaternal females, i.e. ‘allosuckle’, for various reasons. They may compensate (compensation hypothesis) for some nutritional deficiency such as low weight at birth or insufficient supply of maternal milk (Víchová & Bartoš, 2005). Another explanation of allosuckling is that offspring receive a more diverse spectrum of immunoglobulins if they suck from more females (Roulin & Heeb, 1999). The calf may also just use opportunity and learn to suck from nonmaternal females to get some extra energy (Murphey, Paranhos da Costa, Lima, & Duarte, 1991).

Most recent studies support the milk theft hypothesis (Maniscalco et al., 2007; Murphey, Paranhos da Costa, Gomes da Silva, & de Souza, 1995; Zapata, González, & Ebensperger, 2009), misdirected care hypothesis (Boness, Craig, Honigman, & Austin, 1998; Maniscalco et al., 2007; McCracken & Gustin, 1991) or kin selection hypothesis (Bartoš, Vaňková, Šiler, & Illmann, 2001b; Ekvall, 1998; Eberle & Kappeler, 2006), whereas the hypotheses of social benefits (Baldovino & Di Bitetti, 2007), milk evacuation (Wilkinson, 1992) and reciprocity (Engelhardt, Weladji, Holand, Røed, & Nieminen, 2015) are among the less well-documented hypotheses explaining allonursing. However, only a few studies have investigated more than three hypotheses (Engelhardt et al., 2014; Maniscalco et al., 2007).

Giraffes form a fission–fusion social system in the wild (Carter, Seddon, Frere, Carter, & Goldizen, 2013) with several subgroups formed within one herd. These subgroups change according to certain social preferences among the adult females. These preferences may depend on kinship (Bercovitch & Berry, 2013; Malyjurková, Hejzlarová, Jůnková Vymyslická, & Brandlová, 2014). A complex social structure has also been documented in captive giraffes (Bashaw, Bloomsmith, Maple, & Bercovitch, 2007). A dominance hierarchy in the wild has been reported only in bulls (Dagg & Foster, 1976); however, a clear linear age-dependent dominance hierarchy exists in captive giraffe herds (Horová, Brandlová, & Gloneková, 2015). Males live mainly solitarily and associate with females in oestrus (Bercovitch, Bashaw & del Castillo, 2006). Females leave the herd before parturition and give birth (Estes, 1991). Mother and calf join other female giraffes with offspring 1–2 weeks after parturition (Pratt & Anderson, 1979). Calves of similar ages form peer groups, nurseries (crèches), which may be guarded by one of the mothers (Horwich, Kitchen, Wangel, & Ruthe, 1983; Pratt & Anderson, 1979). Guarding of the nursery is a form of alloparental care and therefore provides favourable conditions for the extension of such care to allonursing (Olléová, Pluháček, & King, 2012).

Allonursing has been reported in many mammalian species including even-toed ungulate species in both the wild and captivity (Packer et al., 1992). Studies of captive animals have proven to be insightful for understanding the evolutionary origins of allonursing (Olléová et al., 2012). The few studies on allonursing in giraffes suggest it seldom occurs; however, these studies did not test the hypotheses statistically (Dagg, 1970; Pratt & Anderson, 1979).

In this study, we report for the first time in detail the occurrence of allonursing in giraffes, which is among the highest incidence of allonursing in mammals. We also tested the kin selection, reciprocity, misdirected parental care and milk theft, social benefits, parenting and milk evacuation hypotheses (Table 1).

METHODS

Ethical Note

The observation of giraffes in zoos was carried out from the visitors' area. The observer did not disturb the animals, did not influence their behaviour and did not interfere with the daily management in the stables. Observations were approved by head keepers responsible for the animals in each zoo. No other specific permissions were required.

Study Animals

In total, we observed 24 nursing females and 37 suckling calves of giraffes in four zoological gardens in the Czech Republic: Praha Zoo (six females and 17 calves in 2007–2011), Dvůr Králové Zoo (12 females and 14 calves in 2008, 2009, 2011), Olomouc Zoo (four females and four calves in 2011) and Liberec Zoo (two females and two calves in 2008). We observed the giraffes when two or more calves were present in the herd only; hence, the number of calves simultaneously present in the herd ranged from two to eight.

Twenty-five females gave birth before or during observation at least once. The females gave birth on average once per 20 months. One female gave birth but the calf died. Six females were primiparous (three in 2007 and three in 2011). The calves in all herds were born throughout the year. All calves in each herd in each season were sired by the same bull, making them half-siblings to one another (except in the case of Praha Zoo in 2007 and in 2008, where two breeding herds with calves from two different sires were mixed together).

All giraffes were kept in a stable during most of the winter months, while they spent most of the warm days in the outdoor enclosures. They were fed ad libitum with hay and branches, with limited supplements of granulated food, fruit and vegetables. Females at advanced stages of pregnancy, during and shortly after parturition were separated and fed with milk supplements. Giraffes

Table 1
Hypotheses and predictions of allonursing in giraffes

Hypothesis	Prediction	Statistical model
Kin selection hypothesis	The probability of an allosuckling bout being successful will increase with the coefficient of kinship	Va
Reciprocity hypothesis	Acceptance rate in dyad A will be quantitatively associated with acceptance rate in dyad B	Vb
	Acceptance rate in dyad A will be qualitatively associated with acceptance rate in dyad B	VI
Hypothesis of misdirected parental care	There will be no difference in initiating of filial and nonfilial nursing	I
	The acceptance rate of filial and nonfilial calves will not differ	II
	There will be no difference in the probability of an allosuckling bout being successful when the suckling solicitation involves only one calf (filial or nonfilial)	II
Milk theft hypothesis	Nonfilial calves will try to adopt positions behind the female more often than filial calves	IV
	The filial calf will start multiple nursing more often than a nonfilial calf	III
	The acceptance rate will be higher for filial than for nonfilial calves	II
Hypothesis of social benefits	Females with lower social positions will reject allosuckling solicitation less often than females with higher social positions	II
Parenting hypothesis	The probability of an allosuckling bout being successful will be higher in primiparous than multiparous females	II
Milk evacuation hypothesis	Calves of females that allonursed only a nonfilial calf (without a filial calf present) will not allosuckle from nonmaternal females	

were identified individually by their coat pattern, body size, shape of the horns, shape of the hooves and sex (Estes, 1991).

Data Collection

The data were collected by ad libitum sampling of all suckling events (Altmann, 1974). The observations were conducted every 7–14 days, starting as soon as possible after the birth of the second calf in the herd in the calving season, and finished when the calves were separated from their mothers or when they were weaned (approximately at 12 months of age). Each observation session lasted for 6 h.

During the observation sessions, we recorded all suckling events, including suckling bouts and suckling attempts. A suckling attempt was when the calf took the teat into the mouth for less than 5 s (Drábková et al., 2008), or when the calf just approached the udder of the female closer than the length of the head of the calf (Špinka & Illmann, 1992). The term solicitation was used for suckling attempts and suckling bouts together.

We defined a successful suckling bout as when the calf held the teat in the mouth for 5 s or longer, irrespective of the number of calves simultaneously participating in one nursing. We considered the suckling bout finished when the calf stopped suckling for more than 10 s (Drábková et al., 2008).

For each suckling bout and suckling attempt, we recorded the identity of the nursing female, the identity of the suckling calf, its position (antiparallel, parallel, perpendicular), who initiated (calf/female: the female leads the calf away, sniffs or licks the calf, moves her head towards the udder), who terminated (female/calf/other), number of sucking calves within the suckling bout, order of suckling calves within the suckling bout (which calf came to suckle first, second, etc.), relatedness (filial/nonfilial), sniffing of the calf by the female (yes/no), active rejection of nursing by the female (yes/no) and duration of nursing (s). The parallel and perpendicular positions are thought to prevent lactating females from identifying calves (Bartoš, Vaňková, Hyánek & Šiler, 2001a; Brandlová et al., 2013; Zapata, González, & Ebensperger, 2009).

We determined social rank in the group according to the Clutton-Brock index (CBI) (Clutton-Brock, Albon, & Guinness, 1984). The CBI was calculated using the formula described by Gammell, De Vries, Jennings, Carlin, and Hayden (2003): $\text{CBI} = (B + \sum b + 1)/(L + \sum l + 1)$, where B represents the number of individuals that i defeated in one or more interactions, $\sum b$ represents the total number of individuals (excluding i) that those represented in B defeated, L represents the number of individuals by which i was defeated and $\sum l$ represents the total number of individuals (excluding i) by which those represented in L were defeated (Horová et al., 2015).

Statistics

Data were analysed using the SAS system, version 9.4 (SAS Institute Inc., Cary, NC, U.S.A.). We used an analysis of categorical repeated measurements based on the generalized estimating equation approach (Liang & Zeger, 1986), using logistical regression (GENMOD procedure). To verify the hypotheses of misdirected parental care and milk theft, social benefits, parenting and milk evacuation, we performed four analyses in which we tested the probability that (1) the suckling bout was initiated by the female, (2) the suckling bout was successful (i.e. not rejected by the female), (3) the calf started the bout and (4) the suckling occurred in the perpendicular or parallel position. The independent variables were relatedness (filial, nonfilial calf), herd identity, age of the calf (in months), success of the bout (successful bout, unsuccessful attempt), parity of the nursing female (1–11), the age of the nursing female (5–23 years), hierarchy rank difference between the nursing female and the calf's own mother (lower, higher), the order of suckling calves within the suckling bout (1–6), the position of the suckling calf (antiparallel/perpendicular and parallel) and their first-order interaction terms. The overview of the variables and their inclusion in each statistical model are shown in Appendix Table A1.

To verify the kin selection and the reciprocity hypotheses, we analysed the acceptance rate in female-calf dyads (models V and IV). Dyads involving filial offspring were excluded from these analyses. For each possible dyad (dyad A), we counted this acceptance rate as the number of successful suckling bouts divided by the sum of these bouts and unsuccessful attempts rejected. We introduced a new variable ‘kinship’, which included Wright's coefficient of relatedness (r; Wright, 1922) calculated for each calf-female dyad based on studbook data. Using a general linear model (GLMM, PROC MIXED, SAS), we tested whether the acceptance rate in the dyad was affected by kinship, female parity, herd identity and/or season (model Va). To test reciprocity, we added the acceptance rate of the reciprocal dyad (dyad B; e.g. when dyad A = calf A and female B, the reciprocal dyad B = calf B and female A) to the independent variables and limited the data set to include each dyad pair only once (model Vb).

In addition, we examined whether allonursing occurred at least once between reciprocal dyads (A and B; model VI). Again, we applied logistic regression (GENMOD procedure) using allonursing within dyad A (yes, no) as the dependent variable and allonursing within dyad B (yes, no), kinship of dyad A, female's parity, herd identity and/or the season as independent ones.

To quantify how evenly successful allonursing was spread by each individual to every other potential individual, we used the standardized Shannon–Wiener diversity index (H') (Newton-Fisher & Lee, 2011; Silk, Seyfarth, & Cheney, 1999): $H' = -(p_i \times \ln p_i + p_{i+1} \times \ln p_{i+1} + p_{i+2} \times \ln p_{i+2} + \ldots\ldots + p_n \times \ln p_n)\,/(\ln n - 1)$, where p_i is the relative proportion of allonursing directed towards the ith individual's calf, and n is the number of calves in the group. This index varies from 0 (allonursing focused on a single partner's calf) to 1 (allonursing spread evenly across all potential partners' calves). To verify whether there is any correlation between the Shannon–Wiener diversity index and parity, age of the female or number of females in the herd we used Spearman correlation.

Repeated measures on the same female (models I–III, V, VI) or calf (model IV) were handled with the individual (allo)nursing female entering the model as a subject in the repeated statement. We started with the full model including all of the fixed effects and sequentially dropped those effects that were not significant.

RESULTS

In total, we recorded 2514 interactions including 1644 (65.4%) unsuccessful suckling attempts and 870 (34.6%) suckling bouts, of which 381 (43.8%) included a nonfilial calf (allosuckling bouts). In total, 20 of 24 individual females were observed (representing 83%) allonursing one or more nonfilial calves. Similarly, 32 (86.5%) of 37 calves succeeded in allosuckling from one or more nonmaternal females (Table 2). In 385 cases the suckling bout involved one calf only, of which 290 cases (75.3%) were filial. Multiple nursing occurred 189 times, including the nursing of two calves in 106 cases, the nursing of three calves in 65 cases, the nursing of four calves in 13 cases, the nursing of five calves in four cases and one case of nursing six calves simultaneously. Only in five cases did multiple nursing occur without the filial calf. Of the calves of females that allonursed just a nonfilial calf (without the filial calf present) at least once, 87.5% allosuckled a nonmaternal female (Appendix Table A2).

There were 131 possible dyads of female and nonfilial calf; in 74 of them allonursing occurred at least once, in 32 the calf attempted to allosuckle without success, and in 25 no solicitation was recorded. There were 56 possible reciprocal dyads. The Shannon–Wiener diversity index (H') ranged between 0 and 0.94768 (mean = 0.43 ± 0.31). The Shannon–Wiener diversity index did not correlate with parity, age of the female or the number of females in the herd. Shannon–Wiener indexes for each female are given in Appendix Table A3.

Initiation of Nursing by Females: Model I

The females initiated 105 of 2514 suckling bouts and attempts. They initiated more suckling bouts (10.8%, $N = 870$) than suckling attempts (0.7%, $N = 1644$; $\chi^2_1 = 9.38$, $P < 0.005$; estimate [suckling bouts]: −1.5339; SE: 0.3871; 95% confidence limits: −2.2926, −0.7752) and more suckling events of filial (6.0%, $N = 999$) than nonfilial offspring (1.4%, $N = 1515$; $\chi^2_1 = 6.63$, $P = 0.01$; estimate [nonfilial]: 2.9735; SE: 0.3313; 95% confidence limits: 2.3242, 3.6228). The initiation by females tended to decrease with the increasing age of calves ($\chi^2_1 = 3.55$, $P = 0.06$; estimate: −0.0771; SE: 0.0395; 95% confidence limits: −0.1546, 0.0004).

Probability of Successful Nursing Bouts: Model II

The probability that the suckling bout was successful (i.e. not rejected by the female) was affected by relatedness ($\chi^2_1 = 7.53$, $P < 0.01$; estimate [nonfilial]: −0.4575; SE: 0.1762; 95% confidence limits: −0.8028, −0.1120), the order of suckling calves ($\chi^2_1 = 6.04$, $P < 0.05$; estimate: 1.7990; SE: 0.1908; 95% confidence limits: 1.4250, 2.1730), by female parity ($\chi^2_1 = 6.42$, $P < 0.05$; estimate: 0.1041; SE: 0.0271; 95% confidence limits: 0.0510, 0.1572), and by position ($\chi^2_1 = 5.02$, $P < 0.05$; estimate [antiparallel]: −0.4575; SE: 0.1762; 95% confidence limits: −0.8028, −0.1120). The only nonsignificant variable left in the final model was the herd identity ($\chi^2_{10} = 16.40$, $P = 0.09$). It was not affected by kinship or social rank. In contrast to our predictions, nonfilial calves were more successful (38.1%, $N = 999$) than filial ones (32.3%, $N = 1515$). The probability of successful suckling was higher from antiparallel (37.5%, $N = 1598$) then from parallel or perpendicular (29.6%, $N = 916$) positions, and it increased with increasing order of suckling calves (Fig. 1) and with increasing female parity (Fig. 2).

When only suckling solicitations involving one calf were considered, the probability of successful suckling was affected by relatedness only ($\chi^2_1 = 5.33$, $P < 0.05$; estimate [nonfilial]: −0.5108; SE: 0.3105; 95% confidence limits: −1.1192, 0.0977). Nevertheless, in this case the filial calves were more successful (13.9%, $N = 1238$) than nonfilial ones (4.5%, $N = 611$).

When only suckling solicitations involving nonfilial calves were considered, the probability of successful suckling was affected by the order of suckling calves ($\chi^2_1 = 6.55$, $P < 0.05$; estimate: 1.8079; SE: 0.2024; 95% confidence limits: 1.4111, 2.2046), and by female parity ($\chi^2_1 = 4.16$, $P < 0.05$; estimate: 0.1082; SE: 0.0281; 95% confidence limits: 0.0532, 0.1632).

Table 2
Overview of allonursing in giraffes in individual herds in individual zoos

Herd	Year	Number of nursing bouts	Filial nursing bouts	Nonfilial nursing bouts	Number of allonursing females	Number of allosuckling calves
Dvur	2009	16	11	5	3/3	3/4
Liberec	2008	11	6	5	2/3	1/2
Olomouc	2011	47	36	11	2/4	2/4
Praha	2009	101	51	50	5/5	5/5
Praha	2010	110	53	57	5/5	6/6
Praha	2011	201	113	88	5/5	3/4
Praha Herd 1	2007	34	14	20	3/3	3/3
Praha Herd 1	2008	53	23	30	3/3	2/3
Praha Herd 1	2009	20	17	3	2/2	2/2
Praha Herd 2	2007	27	16	11	3/3	2/4
Praha Herd 2	2008	67	41	26	3/3	5/5
Praha Herd 2	2009	29	16	13	3/4	4/4
Dvur Herd 1	2011	90	50	40	4/6	5/5
Dvur Herd 2	2011	64	42	22	4/5	4/5

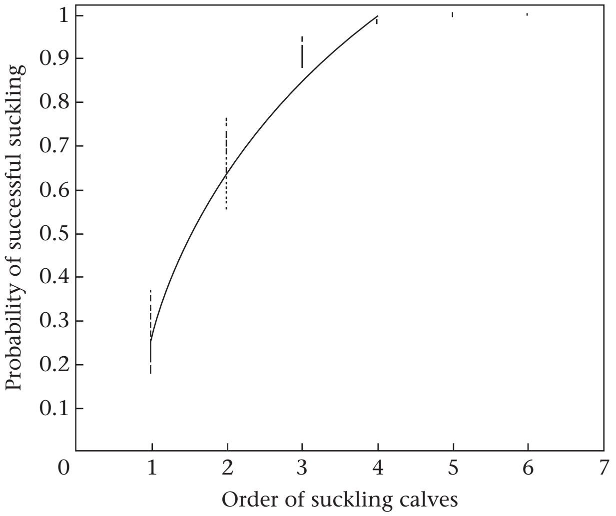

Figure 1. The probability of successful suckling in relation to the order of suckling calves within the suckling bout (which calf came to suckle first, second, etc.; 1–6).

Which Calf Started Suckling? Model III

In this analysis, we considered only successful suckling bouts. We found that filial calves were the first to suckle within the same bout more often (93.3%, $N = 489$) than nonfilial ones (32.6%, $N = 381$; $\chi^2_1 = 8.29$, $P < 0.005$; estimate [nonfilial]: −3.1889; SE: 0.2894; 95% confidence limits: −3.7560, −2.6218). The calves that were the first to start a suckling bout (order of suckling calves = 1) tended to be younger ($\chi^2_1 = 3.30$, $P = 0.069$; estimate: −3.1889; SE: 0.2894; 95% confidence limits: −3.7560, −2.6218) than calves that joined the bout (order of suckling calves = 2 and more).

Suckling Position: Model IV

The probability that a calf adopted the parallel and perpendicular positions, which are more difficult for the lactating female to see, was related to the bout's success ($\chi^2_1 = 6.26$, $P < 0.05$; estimate [successful bouts]: −0.5839; SE: 0.1463; 95% confidence limits: −0.8706, −0.2973) and by the interaction between relatedness and success ($\chi^2_1 = 5.50$, $P < 0.05$; estimate: 0.5929; SE: 0.1977; 95% confidence limits: 0.2053, 0.9804; the relatedness itself had a marginal effect: $\chi^2_1 = 3.76$, $P = 0.053$). It was higher in unsuccessful attempts (39.2%, $N = 1644$) than in successful bouts (31.2%, $N = 870$). In filial calves this probability was higher in unsuccessful attempts (38.1%, $N = 1026$) than in successful bouts (25.6%, $N = 489$; $z = -3.99$, $P < 0.0001$; estimate: −0.5839; SE: 0.1463), and for successful bouts this probability was higher for nonfilial (38.3%, $N = 381$) than for filial calves (25.6%, $N = 489$; $z = 3.00$, $P < 0.01$; estimate: 0.5929; SE: 0.1977).

Acceptance Rate in Female-calf Dyads: Model V

We found that the acceptance rate within female-calf dyads was affected only by female parity ($F_{1,101} = 5.71$, $P < 0.05$; solution for fixed effect: estimate: 0.03225; SE: 0.01350, $_{108} = 2.39$). The acceptance rate within the dyad increased with increasing parity of the female (Fig. 3). No other factor, including kinship within the dyad, affected this rate. When we compared the acceptance rate between all possible reciprocal dyads ($N = 56$ pairs), we did not find any significant results.

Probability of At least One Allosuckling within Female-calf Dyad: Model VI

Nevertheless, comparing the occurrence of allosuckling within all possible reciprocal dyads, we found that in 22 dyads allosuckling occurred at least once in both dyads, in 18 dyads the allosuckling occurred in one dyad only and in 16 dyads no allosuckling was recorded within either dyad (Appendix Table A4). Thus, the probability that the calf within dyad A successfully allosuckled at least once was higher when the calf within dyad B successfully allosuckled at least once also (66.7%, $N = 33$) than when it did not allosuckle (40.0%, $N = 30$; $\chi^2_1 = 4.92$, $P < 0.05$; estimate [unsuccessful allosuckling in dyad B]: −1.3475; SE: 0.5436; 95% confidence limits: −2.4131, −0.2820). The herd identity was also significant ($\chi^2_2 = 6.61$, $P < 0.05$; estimate [Dvůr Králové]: −2.228; SE: 0.7023; 95% confidence limits: −3.5993, −0.8463; estimate [Olomouc]: −1.5680; SE: 1.9086; 95% confidence limits: −3.7212, −0.5853).

DISCUSSION

Although allonursing in giraffes has been recorded before (Dagg, 1970; Pratt & Anderson, 1979), our study is the first to examine it in detail. We found that more than 80% of observed females allonursed, more than 86% of calves allosuckled successfully and 43% of all nursing bouts involved nonfilial calves. Thus, our findings represent the highest rates of allonursing that have ever been recorded among mammals, except for a study on domestic buffaloes, *Bubalus bubalis* (Murphey et al., 1995; for other studies on ungulates see Table 3). Since domestic buffaloes have been selected for milk production, the allonursing rate in captive giraffes is the highest among

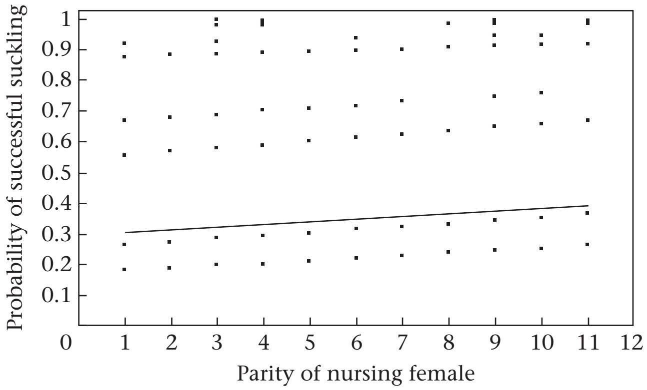

Figure 2. The probability of successful suckling in relation to the parity of the nursing female, i.e. the lifetime number of the female's offspring including current offspring.

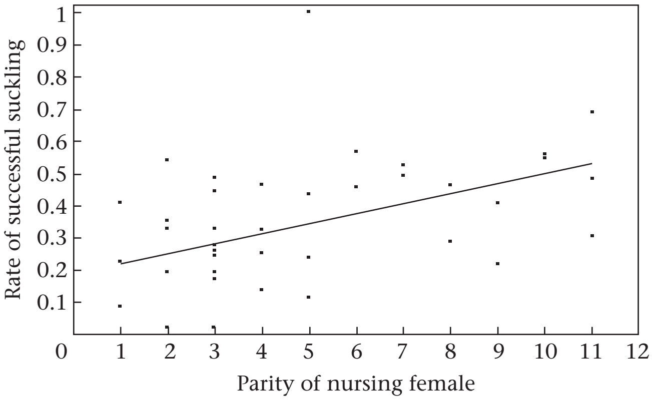

Figure 3. The acceptance rate within the dyad in relation to the parity of the female, i.e. the lifetime number of the female's offspring including current offspring.

nondomesticated mammals overall. Although allonursing in giraffes has not been frequently documented in the wild, its incidental occurrence and apparent attempts have been observed by field researchers from different localities (Kenya, Z. Muller, personal communication; Namibia, J. Fennessy, personal communication; Zambia, F. Bercovitch, personal communication) and in the introduced population of giraffes in Senegal (M. Gloneková, personal observation), suggesting that such behaviour appears across a wide range of environmental conditions. Therefore, giraffes may be a very suitable species for testing various hypotheses on allonursing.

Most of our findings supported the milk theft hypothesis as the most likely explanation of allonursing in giraffes. The nonfilial calves allosuckled more often with the filial calves than alone. This coincides with previous reports on allonursing in giraffes (Dagg, 1970; Pratt & Anderson, 1979) which concluded that ‘when one calf was suckled usually the others were attracted and tried to nurse from the suckling mother’ (Pratt & Anderson, 1979, p. 240), thus that the best way for a calf to allosuckle was to join a suckling pair. The suckling of nonfilial calves mostly together with the filial calf rather than alone has also been observed in other studies favouring the milk theft hypothesis (camels, *Camelus bactrianus*, Brandlová et al., 2013; captive guanacos, Zapata, González, & Ebensperger, 2009).

According to our results, calves approaching a female from parallel and perpendicular positions were less likely to be successful than those approaching from an antiparallel position. In addition, if the nonfilial calves succeeded, they were more likely to be further from the female's head in parallel and perpendicular positions rather than in the antiparallel position adopted mostly by filial calves. These findings suggest that nonfilial calves were most successful when adopting the positions further from the female's head, where they may be harder to recognize and refuse, as reported in other studies supporting the milk theft hypothesis (Brandlová et al., 2013; Zapata, González, & Ebensperger, 2009).

Giraffe calves apparently try to take advantage of any opportunity to suckle milk from any female. Nevertheless, the milk theft hypothesis itself cannot explain the rather high tolerance of giraffe females to allonursing. Of all the tested hypotheses (which need not be mutually exclusive; Roulin, 2002) our results seem to slightly favour the reciprocity hypothesis. The probability that the calf within dyad A successfully allosuckled at least once was higher when the calf within dyad B successfully allosuckled at least once as well. However, there was no evidence that if the female allonursed more, her calf received more. We ascribe this result to the fact that a giraffe female cannot determine how much milk her calf has received from another female, but she is able to identify from which female her calf received the milk. Therefore, our findings are not in line with biological market theory (Noë & Hammerstein, 1994). This may be for several reasons: the costs of allonursing in captivity may be lower, giraffe females may not be selected to count how often their calves are rejected by other females or the qualitative value of the milk transferred from nonmaternal females may be of higher benefit than the quantity.

According to the hypothesis of misdirected parental care, the female should not distinguish between filial and nonfilial calves (Boness, 1990; Cassinello, 1999; Nuñez et al. 2013). We found that the females initiated more nursing events of filial than nonfilial offspring and therefore could probably distinguish between them. However, to our surprise nonfilial calves were more successful when solicited than filial calves suggesting support of the hypothesis of misdirected parental care. On the other hand, when only bouts involving one calf were considered, the filial calves were more successful than nonfilial ones and filial calves started suckling bouts more often than nonfilial ones. The acceptance of the nonfilial calf that started the successful suckling bout could be explained by the reciprocity hypothesis. Some females gave preference to certain nonfilial calves and initiated nursing of them. Sometimes the female initiated nursing of the filial calf while the calf was lying down, and the filial calf could therefore be slower than a nonfilial one standing nearby. Thus, it is likely that females identified calves that arrived first to suckle and in these cases they accepted the filial calf more often than a nonfilial one. Nonfilial calves were therefore more successful when joining an existing bout than when starting it. Since filial calves rarely joined suckling bouts ($N = 33$ cases, 7% of successful suckling performed by filial calves), the higher rejection rate of filial than nonfilial calves could be explained by a higher rejection rate of the calf starting the bout. These findings show that the female distinguished between filial and nonfilial calves and that the different strategies of these calves were clearly in favour of the milk theft hypothesis but not in line with the hypothesis of misdirected parental care.

A wider problem in the milk theft literature (for a review see MacLeod & Lukas, 2014) is whether it is actual ‘theft’ without the nursing female realizing it is not her offspring, or whether females tolerate other offspring, perhaps because the costs are low, as we suggest later. Our study provides a nice example to illustrate that in this case the tolerance is key not lack of recognition as it may be in other studies (Maniscalco et al., 2007; Murphey et al., 1995). To investigate whether giraffes allonurse one individual more than another or allonurse all individuals equally, we used the Shannon–Wiener diversity index. We found that allonursing in giraffes showed extremely large interindividual variability when compared with other frequently allonursing ungulates (Engelhardt et al., 2015). The average values were low. Thus, the giraffes did not focus on a single partner's calf but also did not spread their allonursing evenly across all potential partners' calves. However, this does not exclude reciprocity, as the number of ‘partner’ dyads may vary greatly between individuals. This uneven distribution of dyadic preferences is in agreement with recent findings on giraffe kinship, where the social preferences are also not distributed evenly among herd members (Bashaw et al., 2007; Bercovitch & Berry, 2013; Malyjurková et al., 2014). On the other hand, we cannot exclude the possibility that the slight support for reciprocity found in our study could be an artefact of the high overall incidence of allonursing among the observed giraffes.

Most previous studies examining allonursing found no evidence for the reciprocity hypothesis (Bartoš, Vaňková, Hyánek, & Šiler, 2001a; Murphey et al., 1995; Pusey & Packer, 1994). However, two recent studies supported reciprocity as an explanation of allonursing (Engelhardt et al., 2015; Jones & Treanor, 2008). Nevertheless, in the case of allonursing in bison (Jones & Treanor, 2008), where two females gave birth within 1 h of each other at the same location and shared the care of each other's calf, adoption (Pluháček, Bartošová, & Bartoš, 2011; Riedman, 1982) seems to be the explanation. The second study (Engelhardt et al., 2015) shows patterns of reciprocal allonursing at both the group level and across bouts and within dyads in captive reindeer, *Rangifer tarandus*. In line with our results, in the case of reindeer, no evidence of quantitative reciprocity in terms of allonursing duration between dyads was found (Engelhardt et al., 2015).

Since the probability of successful suckling did not increase with the coefficient of kinship, our results do not support the kin selection hypothesis. The kin selection hypothesis has been suggested as an explanation of allonursing in many studies (Bartoš, Vaňková, et al., 2001a; Eberle & Kappeler, 2006; Ekvall, 1998) but most of these studies involved communally breeding mammals such as dwarf mongooses, *Helogale parvula* (Creel & Rabenold, 1994) or mice, *Mus domesticus* (König, 1994), or mammals forming matrilineal groups (Eberle & Kappeler, 2006) unlike the giraffe. The

Table 3
Overview of allonursing in ungulates

Species	Allonursing as a percentage of all observed nursing (N=number of allosuckling bouts)	Number of allosuckling calves/total number of calves	Number of allonursing females/total number of females	Source
Bison, *Bison bison*	NA	2/2	2/2	Jones and Treanor (2008)
Cattle, *Bos primigenius*	19	15/18	NA/21	Víchová and Bartoš (2005)
Water buffalo, *Bubalus bubalis*	NA	NA	13/14	Murphey et al. (1991)
Water buffalo, *Bubalus bubalis*	50 (N=351)	30/31	13/30?	Murphey et al. (1995)
Camel, *Camelus bactrianus*	8.6 (N=32)	5/10	6/9	Brandlová et al. (2013)
Red deer, *Cervus elaphus*	36 (N=325)	25/39	NA	Bartoš, Vaňková, et al., 2001a
Red deer, *Cervus elaphus*	8 (N=128)	26/38	22/26	Drábková et al. (2008)
Fallow deer, *Dama dama*	43 (N=125)	16/NA	13/16	Ekvall (1998)
Plains zebra, *Equus quagga*	27 (N=113)	1/5	1/4	Pluháček et al. (2011)
Feral horse, *Equus caballus*	NA	1/1	1/1	Nuñez et al. (2013)
Feral horse, *Equus caballus*	NA	1/113	1/NA	Cameron, Linklater, Stafford, and Minot (1999)
Grevy's zebra, *Equus grevyi*	0.8 (N=13)	5/8	7/8	Olléová et al. (2012)
Guanaco, *Lama guanicoe*	5.3 (N=NA)	NA	6/15; 9/14	Zapata, González, & Ebensperger, 2009
Guanaco, *Lama guanicoe*	5.7 (N=84)	9/15; 10/14	6/15; 9/14	Zapata, Correa, Soto-Gamboa, Latorre, González, and Ebensperger (2010)
Warthog, *Phacochoerus africanus*	NA	NA	NA	Plesner Jensen, Siefert, Okori, and Clutton-Brock (1999)
Reindeer, *Rangifer tarandus*	NA	22/25	25/25	Engelhardt et al. (2015)
Reindeer, *Rangifer tarandus*	21 (N=1389)	23/25	25/25	Engelhardt et al. (2014)
Domestic pig, *Sus scrofa domesticus*	17.4 (N=74)	18/191	NA	Illmann, Pokorná, and Špinka (2007)
Giraffe, *Giraffa camelopardalis*	43.8 (N=381)	38/42	20/24	
Common hippopotamus, *Hippopotamus amphibius*	15.5% (N=71)	1/1	1/1	Pluháček and Bartošová, 2011

NA = data were not available.

evolution of cooperative breeding is often associated with kin selection (Clutton-Brock, 2002).

We found that the probability of a suckling bout being successful increased with an increasing number of suckling calves. This means that the female decides whether to allow or prevent suckling mostly when the first calf arrives and when she accepts a calf she does not differentiate that from other calves (allo)suckling from her. Our finding corresponds with the situation described in camels (Brandlová et al., 2013) in which allosuckling was more likely with an increasing number of suckling calves. This result suggests that an increasing number of calves does not bring extra costs for the female, as the amount of milk produced for one nursing bout is limited by the capacity of the udder. On the other hand, our finding differs from that reported recently for reindeer in which females often accepted the calf that arrived second but not those that tried to join later (Engelhardt et al., 2014).

Since the probability that the suckling bout was successful (i.e. not rejected by the female) was not affected by the social rank of the female, our results do not correspond with the hypothesis of social benefits which assumes that adult females can obtain social benefits by allonursing a dominant female's young (Baldovino & Di Bitetti, 2007; Riedman, 1982).

If a female allonursed because she had to evacuate surplus milk, her calf should be satiated and should not need to satisfy its energetic needs by allosuckling (Víchová & Bartoš, 2005). The fact that the majority of calves whose mother allonursed nonfilial calves (14 of 16 cases; Appendix Table A3) did allosuckle suggests that their needs were not fulfilled and therefore our results are inconsistent with the milk evacuation hypothesis. On the other hand, we recorded 95 cases of nursing only nonfilial offspring, representing more than 10% of all successful suckling bouts, and the milk evacuation hypothesis is a possible explanation for this. Thus, although this hypothesis seems to be an unlikely explanation of allosuckling in giraffes, we cannot reject it.

Similarly, the parenting hypothesis was not supported by our results. Indeed, we found the opposite: multiparous females allonursed more often than primiparous ones, as in wild fallow deer, *Dama dama* (Ekvall, 1998). This result may be explained by residual fitness theory (Lessells, 1998). According to this theory, more experienced mothers could provide more milk than less experienced ones. Therefore, when plenty of resources are available (as in captive conditions), the more experienced females could be more tolerant towards nonfilial offspring than less experienced ones (Clutton-Brock et al., 1984).

In conclusion, we report one of the largest occurrences of allonursing in mammals. Based on our results, allonursing in giraffes may be explained mostly by the milk theft hypothesis. In addition, we also found evidence supporting the reciprocity hypothesis to some extent and we did not disprove the milk evacuation hypothesis. This might be important as reciprocity is not favoured by most studies on allonursing.

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Appendix

Table A1
Overview of statistical models including all independent variables involved in the full model

Model number	Procedure	Dependent variable	Independent variables																		
			Relatedness	Age of calf	Age of nursing female	Herd identity	Season	Observer	Success of bout	Parity of nursing female	Sex of calf	Order of suckling calf within suckling bout	Position in suckling	Hierarchy rank of female	Hierarchy rank difference between nursing female and calf's own mother	Success of bout* relatedness	Success of bout* order of suckling calf	Relatedness* order of suckling calf	Kinship	Rate of allonursing in dyad B	Allonursing within dyad B
I	GENMOD	Initiation of suckling	X	X	x	x	x		X	x	x	x	x			x	x				
IIa	GENMOD	Success of bout	X	x	x	X	x	x		X	x	X	X	x	x			x			
IIb	GENMOD	Success of bout	X		x	x	x	x		x	x		x	x	x			x			
IIc	GENMOD	Success of bout		X	x	x	x	x		X		X	X	x	x						
III	GENMOD	Calf suckling in first	X	X	x	x	x	x		x			X	x	x						
IV	GENMOD	Position	X	x	x	x	x	x	X	x	x	x				X	x	x			
V	GLMM	Rate of allonursing in dyad A				x	x			X									x	x	
VI	GENMOD	Allonursing within dyad A				X	x			x									x		X

x indicates variables involved in the initial model and dropped as nonsignificant during the procedure, X indicates variables left in the final model. Model IIb included only those bouts for which one calf was present; models IIc, V and VI included only solicitations made by nonfilial calves.

Table A2
Overview of females that allonursed a nonfilial calf at least once without the filial calf being present and the allosuckling behaviour of their filial calves

Herd	Year	Female	Filial calf	Solicitations to mother/solicitations to nonmaternal female	Attempts with mother/ attempts with nonmaternal female	Allosuckled successfully in other female
Dvur	2011	Brindisi[*]				
Praha	2010	Diana	Sofie	119/51	100/41	Yes
Praha	2007	Eliska	Mahulena	106/7	77/6	Yes
Praha	2009	Eliska	Jirik	147/55	116/43	Yes
Praha	2010	Eliska	Frantisek	178/13	155/12	Yes
Praha	2011	Jaruna	Johan	18/12	9/7	Yes
Praha	2007	Kleopatra	Ludek	63/40	46/27	Yes
Praha	2009	Kleopatra	Gabriela	159/60	117/53	Yes
Praha	2010	Kleopatra	Doubravka	200/5	149/3	Yes
Dvur	2011	Lydie	Lukrecie	34/3	23/1	Yes
Liberec	2008	Nancy	Nisa	13/0	7/0	No
Dvur	2008	Nina	Noel	8/1	1/0	No
Praha	2007	Nora	Sandra	97/35	83/25	Yes
Praha	2009	Nora	Bedriska	54/35	28/38	Yes
Liberec	2008	Sulika[†]				
Dvur	2011	Tootsie	Tim	19/12	11/10	Yes
Olomouc	2011	Veronika	Vambua	92/29	73/24	Yes
Olomouc	2011	Zaira	Zainabu	17/22	14/18	Yes

[*] Pregnant female without calf in the herd at that time.

[†] Female with subadult calf in the herd at that time.

Table A3
Overview of the standardized Shannon–Wiener diversity index (H') for each allonursing female

Female	Herd	Year	Members of herd	Calves in herd	Females in herd	Shannon–Wiener diversity index (H')	Parity of female	Age of female (years)
Berta	Praha	2007	9	5	3	0.61	10	20
Berta	Praha	2009	8	4	4	0.92	11	22
Berta	Praha	2010	12	7	5	0.38	11	23
Brindisi	Dvur Herd 1	2011	12	6	5	0.43	7	21
Diana	Praha	2008	10	6	4	0.66	1	5.5
Diana	Praha	2009	8	4	4	0.86	2	7
Diana	Praha	2010	12	7	5	0.47	2	8
Diana	Praha	2011	9	4	5	0.39	3	8
Eliska	Praha	2008	10	6	4	0.54	3	12
Eliska	Praha	2009	8	4	4	0.95	4	13
Eliska	Praha	2010	12	7	5	0.31	4	14
Eliska	Praha	2011	9	4	5	0	5	16
Etola	Dvur Herd 2	2011	11	6	5	0.31	5	10
Jaruna	Dvur Herd 2	2011	11	6	5	0.63	6	12
Jaruna	Dvur	2009	7	4	3	0	5	14
Julie	Dvur Herd 1	2011	12	6	5	0	3	8
Kasunga	Praha	2007	9	5	3	0.46	1	8
Kenia	Dvur	2009	7	4	3	0	4	10
Kimi	Dvur Herd 2	2011	11	6	5	0.04	9	22
Kleopatra	Praha	2007	9	5	3	0.77	7	15
Kleopatra	Praha	2010	12	7	5	0.44	8	17
Kleopatra	Praha	2011	9	4	5	0.49	8	18
Lydie	Dvur Herd 1	2011	12	6	5	0.65	3	9.5
Nina	Dvur	2009	7	4	3	0	5	11
Nora	Praha	2008	10	6	4	0.75	2	8
Nora	Praha	2009	8	4	4	0.94	3	9
Nora	Praha	2010	12	7	5	0.41	3	10
Tootsie	Dvur Herd 1	2011	12	6	5	0.65	6	16
Veronika	Olomouc	2011	8	5	3	0.33	9	22
Viktoria	Dvur Herd 2	2011	11	6	5	0	3	10
Zaira	Olomouc	2011	8	5	3	0	2	8

Members in herd = all members in the herd at a given time including the adult male and all subadult individuals.

Table A4
Overview of dyadic reciprocity values

Herd	Female A	Calf B	Ratio AB	Female B	Calf A	Ratio BA
Praha	Berta	Bedriska	0.67	Nora	Laura	0.63
Praha	Berta	Dagmar	0.43	Kasunga	Vaclav	0.00
Praha	Berta	Frantisek	0.00	Eliska	Laura	0.27
Praha	Berta	Gabriela	0.67	Kleopatra	Laura	0.25
Praha	Berta	Jirik	1.00	Eliska	Laura	0.27
Praha	Berta	Ludek	0.48	Kleopatra	Vaclav	0.52
Praha	Berta	Mahulena	0.00	Eliska	Vaclav	1.00
Praha	Berta	Slavek	0.67	Diana	Laura	0.44
Praha	Diana	Bedriska	0.50	Nora	Slavek	0.33
Praha	Diana	Doubravka	0.67	Kleopatra	Sofie	0.29
Praha	Diana	Frantisek	0.00	Eliska	Sofie	0.00
Praha	Diana	Jirik	0.50	Eliska	Slavek	0.56
Praha	Diana	Kuba	0.42	Nora	Sofie	0.00
Praha	Diana	Mahulena	0.00	Eliska	Inka	0.00
Praha	Diana	Marek	0.75	Eliska	Inka	0.00
Praha	Eliska	Bedriska	0.39	Nora	Jirik	0.57
Praha	Eliska	Gabriela	0.15	Kleopatra	Jirik	0.10
Praha	Eliska	Kuba	0.12	Nora	Frantisek	0.00
Praha	Eliska	Sandra	0.36	Nora	Marek	0.63
Praha	Kasunga	Gabriela	0.11	Kleopatra	Borek	0.73
Praha	Kasunga	Ludek	0.18	Kleopatra	Dagmar	0.43
Praha	Kasunga	Vaclav	0.00	Berta	Borek	1.00
Praha	Kleopatra	Bedriska	0.50	Nora	Gabriela	0.18
Praha	Kleopatra	Frantisek	0.50	Eliska	Doubravka	0.00
Praha	Kleopatra	Kuba	0.49	Nora	Doubravka	0
Praha	Kleopatra	Slavek	0.00	Diana	Gabriela	0.45
Praha	Nora	Inka	0.75	Diana	Sandra	0.67
Praha	Nora	Mahulena	0.50	Eliska	Sandra	0.36
Praha	Diana	Vaclav	0.00	Berta	Inka	0.00
Praha	Nora	Vaclav	0.00	Berta	Sandra	0.00
Olomouc	Kimberly	Vambua	0.00	Veronika	Kaila	0.00
Olomouc	Kimberly	Zainabu	0.00	Zaira	Kaila	0.00
Olomouc	Zaira	Vambua	0.24	Veronika	Zainabu	0.19
Dvur	Julie	Tim	0.00	Tootsie	Justyna	1.00
Dvur	Julie	Lukrecie	0.00	Lydie	Justyna	0.50
Dvur	Julie	Tanja	0.00	Tanaka	Justyna	0.00
Dvur	Lydie	Tanja	1.00	Tanaka	Lukrecie	0.00
Dvur	Lydie	Tim	0.57	Tootsie	Lukrecie	1.00
Dvur	Tanaka	Tim	0.00	Tootsie	Tanja	1.00
Dvur	Ella	Ozak	0.00	Etola	Legas	0.00
Dvur	Ella	Tery	0.00	Viktoria	Legas	0.50
Dvur	Ella	Edgar	0.00	Etola	Legas	0.00
Dvur	Ella	Johan	0.00	Jaruna	Legas	0.00
Dvur	Ella	Mick	0.00	Kimi	Legas	0.00
Dvur	Viktoria	Edgar	0.00	Etola	Tery	0.00
Dvur	Viktoria	Johan	0.00	Jaruna	Tery	1.00
Dvur	Viktoria	Mick	0.00	Kimi	Tery	0.00
Dvur	Viktoria	Ozak	0.00	Etola	Tery	0.00
Dvur	Etola	Johan	0.50	Jaruna	Edgar	1.00
Dvur	Etola	Mick	0.80	Kimi	Edgar	0.83
Dvur	Jaruna	Mick	1.00	Kimi	Johan	1.00
Dvur	Jaruna	Ozak	0.00	Etola	Johan	0.50
Dvur	Kimi	Ozak	0.00	Etola	Mick	0.80
Dvur	Jaruna	Ali	1.00	Kenia	Jan	1.00
Dvur	Jaruna	Noel	0	Nina	Jan	0
Dvur	Kenia	Noel	0	Nina	Ali	0

Ratio = number of nursing bouts/number of solicitations.

5.2. The First Description of Dominance Hierarchy in Captive Giraffe: Not Loose and Egalitarian, but Clear and Linear

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RESEARCH ARTICLE

The First Description of Dominance Hierarchy in Captive Giraffe: Not Loose and Egalitarian, but Clear and Linear

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Abstract

Wild giraffes live in extensive groups in the fission fusion system, maintaining long social distances and loose social bonds. Within these groups, resources are widely distributed, agonistic encounters are scarce and the dominance hierarchy was reported in males only, while never deeply analysed. In captivity, the possibility to maintain inter-individual distances is limited and part of the resources is not evenly distributed. Consequently, we suggest that agonistic encounters should be more frequent, leading to the establishment of the dominance hierarchy. Based on the differences in resource-holding potential, we suggested that the rank of an individual would be affected by age and sex. Based on hypotheses of prior ownership, we tested whether rank was positively affected by the time spent in a herd and whether it was stable in adult females, which were present long-term in the same herd. We originally monitored four herds of Rothschild giraffes (*Giraffa camelopardalis rothschildii*) in Dvůr Králové zoo (n = 8), Liberec zoo (n = 6), and two herds in Prague zoo: Prague 1 (n = 8) and Prague 2 (n = 9). The Prague 1 and Prague 2 herds were then combined and the resulting fifth herd was observed over three consecutive years (2009, 2010, and 2011) (n = 14, 13, and 14, respectively). We revealed a significantly linear hierarchy in Dvůr Králové, Prague 2 and in the combined herd in Prague. Rank was significantly affected by age in all herds; older individuals dominated the younger ones. In females, rank was positively affected by the time spent in the herd and adult females in Prague maintained their rank during three consecutive years. This study represents the first analysis of the dominance hierarchy in the captive giraffe, and discusses the behavioural flexibility of the social structure in response to monopolisable resources in a captive environment.

Introduction

Life in a group for prey species often evolved as a response to predation pressure [1]. Benefits as increased vigilance, foraging efficiency, and better offspring survival force individuals

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together, in balance with costs that arise from close proximity. The costs of group living are mostly connected with competition, either for mates or resources [1]. Due to this competition, individuals often participate in agonistic interactions. When these interactions are easily identified and repeated in a consistent way, they can be referred to as dominance—subordinate interactions based on a winner and loser effect [2]. These interactions may lead to the establishment of dominance hierarchies that decrease the overall level of agonistic interactions within the group [1], since the subordinate individuals might actively avoid conflict with the dominant ones. The formation of such interactions presumes that an individual can recognise and remember other group members [3]. An individual's rank is mostly used as a measure of its position in the hierarchy [4–6]. Both agonistic ranks based on the interactions and competitive feeding ranks based on differential access to food can be measured and tend to be strongly correlated [7]. The rank orders are mostly sex- and age-dependent [8] and correlate with many behavioural variables, such as reactions to novelty and learning performance [9], and success at foraging and reproduction [10–15]. The dominance rank order however, might reflect the resource-holding potential (RHP) of an individual [16,17]. The resource holding potential is based on the assessment of rival's abilities and probability of the conflict escalation over the resource or withdrawal from the resource. The higher is the difference between rivals, the lower is probability of conflict escalation. Therefore, an individual assesses its rival according to external features (as size or body-mass) and decides whether to enter the conflict or not [17]. Alternatively, the experience of an individual may play role in the hierarchy formation, based on prior ownership. Despite of lower body mass, an individual may be in possession of a resource and develops an effective strategy for its protection. In such a case, the rival approaching a resource may lose despite of larger size or higher body-mass [18,19]. Those two approaches are not mutually exclusive. Once formed, the rank orders can be stable for long periods or continually reassessed. The stability of female social rank over time should provide important benefits as increased reproductive success [20].

Species that live in loose groups with abundant and widespread resources are not expected to establish dominance hierarchies to gain priority access to such an "unlimited" resource [21]. Moreover, interactions that lead to the establishment and maintenance of hierarchies can be stressful to subordinate animals, and might also result in serious or fatal injuries [12,22], suggesting that the hierarchies are formed when such costs are outweighed by benefits gained from priority access to resources. Abundant and widespread resources are typical for the most of wild ungulates, but not for captive ones. In captivity, two types of food are usually provided—forage and concentrates. While the access to the forage is generally unlimited, the concentrates are fed in limited amount per head, and they are generally considered attractive resource. The feeding rank in ungulates is therefore often studied during feeding of concentrates [23–26]. Limited resources in wild giraffes cause changes in females and also males social behaviour [27], while even water may be considered such a limited resource [28], we can therefore expect such a behavioural change also in captive environment.

In the captive environment an individual is unable to leave the group to avoid the interaction, but is forced to stay in the group and deal with its herdmates. Such artificial change of conditions may lead to the expression of behavioural flexibility of the species in the changing environmental conditions [29], corresponding to the presumptions that in the limited space of stables and outdoor enclosures, animals establish a mechanism to prevent inter-individual conflicts over limited resources as the concentrate feeding is [3,30,31]. The ability of a species to exhibit behavioural flexibility to environmental conditions was proved to be important for its survival [29], provides advantages in new environments [30] and during habitat alterations [31].

The giraffe (*Giraffa camelopardalis*) is an example of a prey species with loose social bonds that uses abundant and widespread resources. Social bonds among giraffes have been recently discussed and perceptions of the social system have switched from loose aggregations of individuals with non-lasting social bonds [32–34] to an advanced fission—fusion system with an elaborated communication structure [35–38].

Wild giraffes live in low densities and rarely approach conspecifics, except for feeding at the same tree and maintaining a distance over 20 m apart [32]. Social interactions in wild giraffes are very subtle and are restricted mainly to mother—offspring contact and the agonistic encounters of males [39]. The social life of wild female giraffes has been described as an association of small groups of a few members, which generally includes calves and occasionally some younger males [36,40,41]. Groups are temporary and their size depends on the season [41]. Temporary changes in group size were first explained by Bercovitch and Berry [42], who described giraffe social structure as a fission—fusion system within large groups. This also corresponds with evidence that wild female giraffes form stable populations within an area [40]. The dominance hierarchy has been described for male giraffes only [34] and has not been deeply analysed. The theory that the long neck of a giraffe evolved to gain dominance in sexual encounters [43] has recently been abandoned [44,45].

The Rothschild giraffe (*Giraffa camelopardalis rothschildi*) belongs to the Red List of endangered taxa [46] about which limited knowledge from the wild exists. Rothschild giraffes inhabit dense savannah woodland in Uganda and Kenya with fewer than 1,100 wild individuals remaining. They are successfully bred in captivity mainly in European and US zoos, with numbers exceeding 500 living individuals (according to ZIMS—Zoological Information Management System 2014), thus providing an excellent base for research and conservation.

A recent publication of Bashaw et al. [47] demonstrated that Rothschild giraffes in captivity have a complex social structure. This fact challenges the original opinion that the only strong bonds among giraffes are between a mother and her dependent young [48]. Furthermore, the experimental social separation of captive Rothschild giraffes provided another evidence of complex and long-term relationships of giraffe [49]. Another finding of Bashaw [50] supports the fact that captive giraffes maintain social relationships and suggests that studies of giraffe social relationships and activity are applicable across a range of captivity conditions [51]. However, the dominance hierarchy has never been studied in captive giraffes.

Given that the possibility to maintain social distances in captivity similar to those in the wild is limited by the size of enclosure or stable, the number of social encounters increases. Moreover, the access to preferred food (pellets, vegetables or concentrates) is limited to several occasions throughout the day, resulting in unequally distributed resources. Because of this, we suggest that the benefits of hierarchy formation (priority access to resources) outweigh the costs (risk of injury during agonistic encounters) and (i) the dominance hierarchy will form in captive giraffes. Based on the difference in resource holding potential [16], we presume that the rank of an individual will be affected (ii) by age and (iii) by sex. Captive herds of giraffes are often stable, with unrelated individuals joining the herd only due to breeding management. We presumed that (iv) rank would be positively affected by the time spent in a herd, regarding the asymmetry of prior ownership [18,19] and (v) that rank would be stable among adult females in the periods when no adults enter or leave the herd.

Materials and Methods

Ethic Statement

The observations of giraffes in zoos took place in most cases from the visitors' area. To the breeding facilities the observer came only when it was necessary. The observer did not disturb the animals, did not influence their behaviour or interfere with the daily management in the stables. Behavioural sampling did not affect the animals in any manner. Observations were approved by head zoologists responsible for the animals in each zoo, namely: Jaroslav Šimek, Prague Zoo, Luboš Melichar, Liberec Zoo, and Luděk Čulík, Dvůr Králové Zoo. No other specific permissions were required.

Study Sites and Subjects

Data were collected in captive Rothschild giraffe herds in three zoological gardens in the Czech Republic, namely in Prague Zoo between 2008 and 2011, in Dvůr Králové Zoo in 2010, and in Liberec Zoo in 2010. All observed individuals were born in captivity, as well as their parents. The observations were performed from the visitors′ area or from the keepers′ area when necessary. The observations did not influence the behaviour of the studied animals and observers did not alter the daily routine procedures of husbandry in any zoo.

The zoo enclosures differed in size (Prague Zoo—400 m^2 indoor, 2.2 ha outdoor, Liberec Zoo 700 m^2 indoor, 0.14 ha outdoor, Dvůr Králové Zoo—270 m^2 indoor, 0.22 ha outdoor), but were similar in structure. Each outside enclosure was formed of a sandy surface with grass and several trees. Inside enclosures were littered with sawdust. All herds were fed by forage *ad libitum*, formed by hay or grass accompanied by branches for browsing. Concentrated feed was provided in the form of grain fodder, fresh fruit and vegetables, which was provided twice-daily and consumed immediately. Access to water was provided *ad libitum*.

We originally monitored four herds of Rothschild giraffes (*Giraffa camelopardalis rothschildii*) in Dvůr Králové Zoo (eight individuals), Liberec Zoo (six individuals), and two herds in Prague Zoo: Prague 1 (eight individuals) and Prague 2 (nine individuals). The Prague 1 and Prague 2 herds were then combined and the resulting fifth herd was observed in three consecutive years (2009, 2010, and 2011) as Joined 1 (14 individuals), Joined 2 (13 individuals) and Joined 3 (14 individuals). Adults, sub adults and juveniles were present in all observed herds (S1–S7 Tables). Giraffes have naturally distinctive markings [39] and therefore, all studied animals were identified individually by their coat pattern, body size, shape of the horns, shape of the hooves, and sex.

Data Collection

Data collection occurred during daytime hours. The total time of observation was 240 h in all zoos (Table 1). Agonistic encounters with a clear submissive reaction were recorded into a loss and win table *ad libitum* [52], during feeding. Win and loss table contained information about the identity of each individual, date of the observation, time of the beginning and end of the observation period, who was the winner of the encounter, who was the recipient, what kind of

Table 1. Results of linearity in all studied herds.

Locality	Season	Number of individuals	Number of interactions	Observed hours	Landau's index (h)	Corrected index (h')	*P* value	Hierarchy
Dvůr Králové	2010	8	111	13	0.73	0.74	$P < 0.05$	Linear
Liberec	2010	6	51	10	0.69	0.73	$P > 0.05$	Near-linear
Praha 1	2008	8	118	65	0.56	0.64	$P = 0.08$	Near-linear
Praha 2	2008	9	156	67	0.69	0.73	$P < 0.05$	Linear
Joined 1	2009	14	339	35	0.52	0.56	$P < 0.05$	Linear
Joined 2	2010	13	313	33	0.48	0.53	$P < 0.05$	Linear
Joined 3	2011	14	265	17	0.82	0.84	$P < 0.05$	Linear

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threat it was. We recorded the most apparent forms of aggression, including necking, strikes with the head also described as bumping [53,54], as well as milder forms of aggression, including threats, pushes and chases. Pushes and chases occurred when the aggressor moved directly towards the loser in a line to intercept it, then either remained in the site formerly occupied by the loser, or continued moving through the point of intersection whilst the loser moved away (a chase). Seeber et al. [53] called chase yield, Bashaw [55] called it avoiding. Threat was described as unspecified aggression, Seeber et al. [53] refers to it as displace and Bashaw [55] summarised it as non-contact aggression. Only agonistic interactions were recorded, in which the loser apparently avoided the winner, adopted a submissive posture and did not return to the conflict, as only these interactions demonstrate that the submissive individual accepted its subordinate position. Observations were made until filling the loss and win table.

Data Analyses

To determine whether (i) a hierarchy existed in the captive giraffe herds, we created dominance matrices. These matrices originated from loss and win tables, which were filled in during observations. For each agonistic encounter, the winner and loser were recorded, allowing the calculations of wins and losses for each individual. Loss and win tables were analysed in MatMan software and were compiled by the I&SI method [5]. The aim of the I&SI method is to identify an order that is the most consistent with a linear hierarchy. Firstly, it minimises the number of inconsistencies (dyads for which the actual dominance relationship does not correspond with the relationship in the hierarchy found). Secondly, it minimises the total strength of the inconsistencies SI, subject to the condition that I is at its minimum [56]. We evaluated the transitivity of dominance relationships among group members, based on submissive behaviours. We used de Vries′ improved version of Landau′s index of linearity [57], correcting for unknown and tied relationships (h'). The value of h' varies from 0, indicating absence of linearity, to 1, indicating complete linearity [58,59]. A value h' higher than 0.80 was taken to indicate a strongly linear hierarchy [59].

To test whether (ii) older individuals have a higher rank than younger individuals, (iii) males are higher in rank than females and (iv) individuals that spent more time in a herd are on a higher rank, we calculated Clutton-Brock Index (CBI) [60], as it provides detailed information not only about the order within hierarchy, but also about the relative distances between individuals. The CBI for each member, i, of a group was calculated using the formula described in detail by Gammell et al. [61]: $CBI(\mathrm{i}) = (B + \sum b + 1) / (L + \sum l + 1)$, where B represents the number of individuals that i defeated in one or more interactions, $\sum b$ represents the total number of individuals (excluding i) that those represented in B defeated, L represents the number of individuals by which i was defeated and $\sum l$ represents the total number of individuals (excluding i) by which those represented in L were defeated [61–63]. An individual′s rank range from 1, which is the top rank, and it further goes up to the number of individuals in a group. We also used the CBI rank for comparison of the changes among three consecutive years in the combined herd in Prague.

As the data were not normally distributed, we used logarithmic transformation of CBI values. Transformed CBI values showed normal distribution (Kolmogorov-Smirnov test, $d = 0.14$, $p > 0.2$). All analyses were performed in software STATISTICA 2011 version 9.1. For predictions (ii, iii) we analysed the influence of age and sex on the CBI values using General Linear Model (GLM), with "age" (years) as continuous variable and "sex" (male, female) as categorical variable. We also tested the interaction of "age" and "sex" within the model.

As age and time spent in the herd were correlated, for analysis of (iv) time spent in the herd we used linear regression and we also tested the differences between sexes.

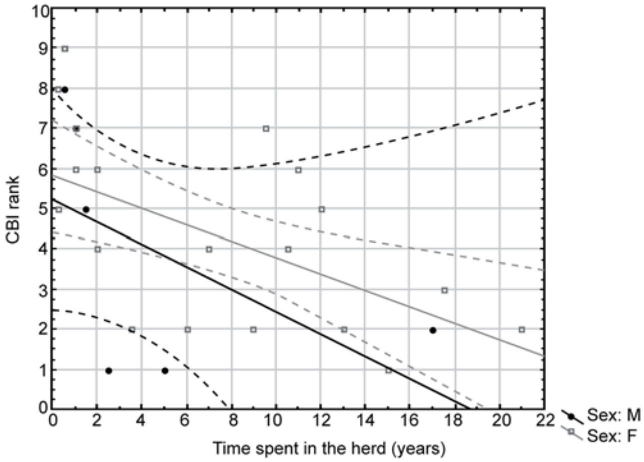

Fig 1. Rank vs. age. The CBI rank was significantly ($F_{(1, 5.168)} = 13.16$, $P < 0.001$) affected by age. Note that the highest rank level is 1 (the first position in a hierarchy).

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Results

In 240 total hours of observation time, 1,353 agonistic interactions were observed between individuals. The dominance matrices of herds in Dvůr Králové and Prague 2 revealed a significant linear hierarchy (i). The dominance matrices of the combined herd Prague revealed a significant linear hierarchy for all three consecutive years. The dominance matrix of the Liberec and Prague 1 herds were near-linear (Table 1).

We confirmed that (ii) CBI values for individual giraffes were significantly ($F_{(1, 5.168)} = 13.16$, $P < 0.001$) affected by age (Fig 1). (iii) Sex did not affect the CBI of mixed giraffe herds neither separately ($F_{(1, 0.007)} = 0.01$, $p = 0.89$) nor in interaction with age ($F_{(1, 0.553)} = 1.4$, $p = 0.25$). (iv) CBI was positively affected by the time spent in the herd ($r^2 = 0.02$, $P < 0.05$) (Fig 2). Further analyse showed that CBI was influenced by time spent in the herd in females only ($r^2 = 0.25$, $p = 0.017$), not in males ($r^2 = 0.35$, $p = 0.09$).

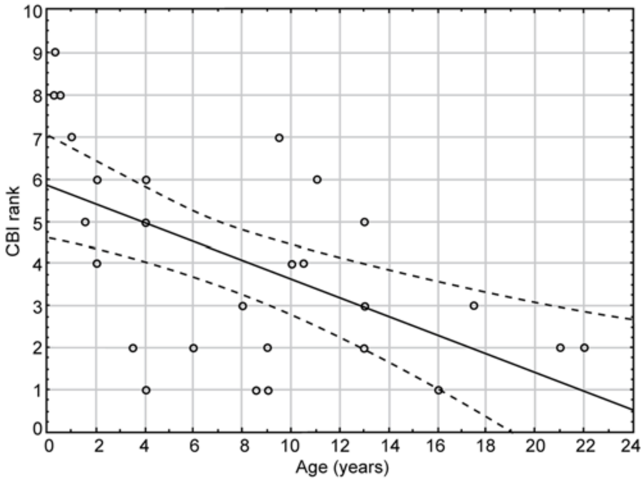

Fig 2. Rank vs. time in a herd. The CBI rank was influenced by time spent in the herd in females only ($r^2 = 0.25$, $p = 0.017$), not in males ($r^2 = 0.35$, $p = 0.09$). Note that the highest rank level is 1 (the first position in a hierarchy).

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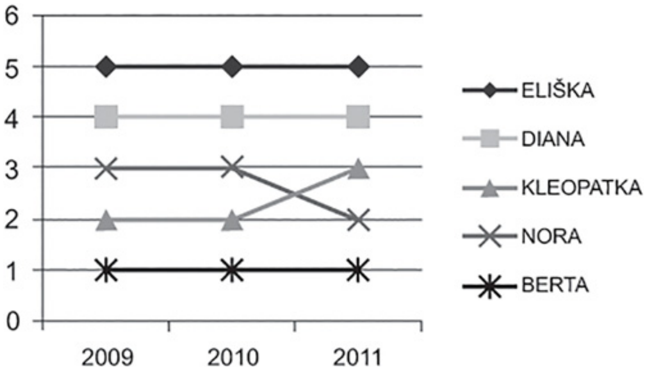

Fig 3. Rank stability. Changes in the CBI rank of five adult females during three consecutive years in the combined herd in Prague.

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(v) Adult females in Prague (herds Joined 1, Joined 2, and Joined 3) maintained their rank during three consecutive years with only one exception of two females that exchanged their positions relative each another (Fig 3).

Discussion

This study represents the first detailed analysis of the dominance hierarchy in the captive giraffe. The dominance hierarchy in wild giraffes has only been reported in bulls, dividing them into three age classes [64]. Nevertheless, studies that focused on the fission—fusion system in giraffes stated that the hierarchy did not exist in giraffes [37] or the studies did not consider the hierarchy or dominance relationships at all [35,36,65]. Neither the studies of social relationships in captive giraffes considered dominance relationship and hierarchy formation [47,49]. However, the dominance hierarchy as a part of social environment may substantially contribute to the formation of social system, together with generally represented ecological factors, and influence the association patterns [66].

Formation of hierarchy in captive Rothschild giraffes corresponds to the presumptions that in the limited space of stables and outdoor enclosures, giraffes establish a mechanism to prevent inter-individual conflicts over limited resources [3,67,68]. Hierarchy formation might help captive giraffes to save energy and prevent the risk of injuries during frequent interactions [3]. The dominant giraffes gained priority access to food, and had the possibility to select preferred food components as shown by Ceacero et al. [69]. Nevertheless, most of the captive ungulates (both wild and domestic) face similar restriction in space and limited access to concentrated food, which is not common in their natural environment. Despite this, not all of them develop dominance hierarchies in captivity, e.g. camels (KB—unpublished data). The formation of hierarchy in the captive giraffe therefore appears to reflect the behavioural flexibility of the species facing unnatural captive conditions.

The hierarchical structures in observed captive giraffe herds were mostly significantly linear or had high values of linearity indices even when not significant. This is not always the case in ungulate societies, where triangular or complex dominance relationships are common [57,70,71]. The linearity of hierarchies was stronger in larger giraffe herds (8–14 individuals) than in smaller ones (6–8 individuals), in contrary to the findings of Favre et al. [15], where linearity decreased with the increasing size of a herd. Linear hierarchies have been often reported in female-bonded ungulate groups [58,72], which are formed by closely tied and related females. The linearity of the dominance hierarchy in the giraffe supports the findings of recent studies showing that the relationships among female giraffes are stronger than previously thought [47,51].

Similarly to other ungulates, the position in the hierarchy was strongly affected by the age of an individual. In captive Rothschild giraffes, adult individuals dominated subadults and juveniles and the subadults dominated juveniles. Older individuals often occupy the top hierarchical positions in ungulate groups [11,73–75]. Although age is strongly correlated with body mass before individuals reach adulthood, in adult animals, age might have a higher impact than body mass [76]. An age- (and/or body mass) based linear hierarchy was found in other savannah species living in a fission—fusion system, where the resources are abundant, but some scarce patchily distributed resources favoured the establishment of such a hierarchy [58].

We observed no difference between the rank of males and females of the same age class. We observed herds with mixed sexes in all cases, but there was always only one adult male in the herd due to management and safety reasons. It is therefore likely that the lack of effect is a function of the small sample size in case of males. Nonetheless, the rank of the adult male was the highest of all individuals except for one case, even though males were neither the tallest nor the oldest individuals. The mean ranks of juvenile males tended to be higher than that of juvenile females, probably due to the differences in growing patterns and resulting sexual dimorphism [33]. Given the sample size of our studied group, we suggest that sex and/or size might play a role in achievement of the dominance rank, as in Correa et al. [72].

We also suggested that the rank was positively correlated with the time spent in a herd, although there was a confounding effect of age, as the number of individuals joining the herd during adulthood was not sufficient for the detail statistical evaluation. The time spent in a herd was related to the rank of females but not to the rank of males, which further support the existence of stronger bonds among females in the fission fusion system. This finding corresponds with the asymmetries connected with prior ownership [18]. Hierarchies might be based on such asymmetries and respected, even if they do not correspond to the differences in RHP, such as body mass [19]. This might also reflect the fact that older females or females that live for a longer time in an area are better able to maintain their dominance because of experience.

Once established, the hierarchy among adult females appears to be stable, as shown in the combined herd in Prague. All females maintained their ranks during three consecutive years, with one exception: two females with a position in the hierarchy very close to one another exchanged their ranks during the final year of observations. We cannot derive any general conclusion from this case, as this was the only herd that was observed in three consecutive seasons. Nevertheless, this result corresponds very well with a similar situation for other captive ungulates [11,22].

Hierarchy formation in captive giraffes appears to be based on their RHP, although we did not obtain data for body mass or other phenotypic traits that enabled certain individuals to acquire dominance over individuals that are unable to oppose them. However, before adulthood, age in giraffe is strongly correlated with size [77]. After reaching adult size, age becomes independent of physical traits such as body mass or height in giraffes [77]. Age-driven rank position might then lead to hierarchy formation based on mutual benefits from avoiding the conflicts over patchily distributed usurpable resources [58].

The evidence for hierarchy in captive giraffes suggests the existence of behavioural flexibility in an evolutionary old species. Wild giraffes are non-territorial animals [32,78] and rely on abundant, widely distributed resources [79–81], thus, their social relationships might remain unresolved because there is no need to dominate over others in terms of feeding competition [58]. However, although individuals are not constantly together in the fission—fusion system, clear dominance hierarchies among society members might be formed, to dominate over patchily distributed resources [7,58,66]. Given the decrease in suitable habitats for giraffes and the differential nutritional value of plants in the savannah ecosystem [82], the feeding preferences of individual giraffes might lead to the existence of competitive feeding behaviour in the future, leading to hierarchy formation as shown in the example of captive giraffes. The existence of dominance hierarchies might therefore influence the association patterns and social structure of the giraffe herds [66,83,84]. This pilot study of the hierarchy in captive giraffe herds demonstrates a behavioural change as a response to modified living conditions and suggests the direction for studies in broader sociobiological context.

Conclusions

Although the relationships among giraffes are often described as loose and subtle, we demonstrated that a clear linear dominance hierarchy existed in captive giraffe herds. The rank of an individual was affected by its age and the rank of females was stable during subsequent observational seasons. The establishment hierarchy was based on the resource-holding potential over limited resources in captivity. The characteristics of hierarchy reflected those found in other female-bonded ungulates and the formation of a linear hierarchy in captivity reflected the behavioural flexibility of the giraffe in facing different environmental conditions.

Supporting Information

S1 Table. Composition of herd Prague 1.
(DOCX)

S2 Table. Composition of herd Prague 2.
(DOCX)

S3 Table. Composition of herd Dvůr Králové.
(DOCX)

S4 Table. Composition of herd Liberec.
(DOCX)

S5 Table. Composition of herd Joined1.
(DOCX)

S6 Table. Composition of herd Joined2.
(DOCX)

S7 Table. Composition of herd Joined3.
(DOCX)

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Author Contributions

Conceived and designed the experiments: KB. Performed the experiments: EH. Analyzed the data: KB EH. Contributed reagents/materials/analysis tools: EH KB MG. Wrote the paper: EH KB MG.

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Tables from the article

S1 Table: Composition of herd Praha 1.

Name	Date of Birth	Age (years)	Sex	Category	Rank according CBI
Kleopatra	13.1.1993	16	F	AD	1
Šimon	21.12.1986	22	M	AD	2
Kasunga	2.7.2000	8	F	AD	3
Hana	16.8.2006	2	F	SUB	4
Luděk	26.8.2007	1.5	M	SUB	5
Václav	28.9.2007	1.5	M	SUB	5
Bořek	11.7.2008	1	M	JUV	7
Gabriela	3.3.2009	0.25	F	JUV	8

S2 Table: Composition of herd Praha 2.

Name	Date of Birth	Age (years)	Sex	Category	Rank according CBI
Johan	20.12.1999	9	M	AD	1
Berta	25.3.1988	21	F	AD	2
Eliška	6.10.1995	13	F	AD	2
Nora	27.6.1999	9	F	AD	2
Diana	6.1.2003	6	F	AD	2
Nikola	28.11.1997	11	F	AD	6
Mahulena	17.11.2007	1	F	SUB	7
Slávek	19.1.2009	0.5	M	JUV	8
Bedřiška	1.3.2009	0.25	F	JUV	9

S3 Table: Composition of herd Dvůr Králové.

Name	Date of Birth	Age (years)	Sex	Category	Rank according CBI
Tommy	2.3.2002	8.5	M	AD	1
Jenifer	11.2.2007	3.5	F	AD	2
Nina	12.7.1997	13	F	AD	3
Kenia	2.5.2000	10	F	AD	4
Jaruna	2.7.1997	13	F	AD	5
Johari	5.10.2006	4	F	AD	6
Etola	20.11.2001	9,5	F	AD	7
Ozák	5.1.2010	0.5	M	JUV	8

S4 Table: Composition of herd Liberec.

Name	Date of Birth	Age (years)	Sex	Category	Rank according CBI
Twiga	9.12.2006	3.5	F	AD	1
Miky	24.8.2006	4	M	AD	2
Nancy	30.3.1993	17.5	F	AD	3
Sandra	27.1.2000	10.5	F	AD	4
Vanesa	28.7.2006	4	F	AD	5
Nela	21.4.2008	2	F	SUB	6

S5 Table: Composition of herd Joined 1.

Name	Date of Birth	Age (years)	Sex	Category	Rank according CBI
Johan	20.12.1999	10	M	AD	1
Berta	25.3.1988	22	F	AD	2
Kleopatra	13.1.1993	17	F	AD	3
Nora	27.6.1999	10	F	AD	4
Bořek	11.7.2008	2	M	SUB	5
Faraa	30.10.2007	2.5	F	SUB	6
Nikola	28.11.1997	12	F	AD	7
Diana	6.1.2003	7	F	AD	8
Eliška	6.10.1995	14	F	AD	9
Jiří	28.4.2009	0.75	M	JUV	10
Bedřiška	1.3.2009	0.75	F	JUV	11
Slávek	19.1.2009	1	M	JUV	12
Gabriela	8.3.2009	0.75	F	JUV	13
Laura	30.5.2009	0.5	F	JUV	14

S6 Table: Composition of herd Joined 2.

Name	Date of Birth	Age (years)	Sex	Category	Rank according CBI
Johan	20.12.1999	10.5	M	AD	1
Berta	25.3.1988	22.5	F	AD	2
Kleopatra	13.1.1993	17.5	F	AD	3
Nora	27.6.1999	11	F	AD	4
Faraa	30.10.2007	3	F	SUB	5
Diana	6.1.2003	7.5	F	AD	6
Eliška	6.10.1995	15	F	AD	7
Jiří	28.4.2009	1.25	M	SUB	8
Bedřiška	1.3.2009	1.25	F	SUB	9
Slávek	19.1.2009	1.5	M	SUB	10
Gabriela	8.3.2009	1.25	F	SUB	11
Laura	30.5.2009	1	F	JUV	12
Kuba	24.7.2010	0.08	M	JUV	13

S7 Table: Composition of herd Joined 3.

Name	Date of Birth	Age (years)	Sex	Category	Rank according CBI
Johan	20.12.1999	11	M	AD	1
Berta	25.3.1988	23	F	AD	2
Faraa	30.10.2007	3.5	F	AD	3
Nora	27.6.1999	11.5	F	AD	4
Kleopatra	13.1.1993	18	F	AD	5
Diana	6.1.2003	8	F	AD	6
Eliška	6.10.1995	15.5	F	AD	7
Bedřiška	1.3.2009	2	F	SUB	8
Gabriela	8.3.2009	2	F	SUB	9
Joel	14.10.2010	0.5	M	JUV	10
Laura	30.5.2009	2	F	SUB	11
Kuba	24.7.2010	0.5	M	JUV	12
Doubravka	23.1.2011	0.08	F	JUV	13
Sofi	6.1.2011	0.09	F	JUV	14

5.3. The Weight of Rothschild Giraffe—Is It Really Well Known?

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RESEARCH ARTICLE

The Weight of Rothschild Giraffe—Is It Really Well Known?

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Despite being regularly bred in zoos, giraffes remain a challenge, especially in terms of feeding. Assessment of factors influencing growth and weight changes during ontogeny, as well as analysis of weight fluctuations in adult individuals, may become a critical point in captive diet evaluation. Knowledge about weight is a crucial husbandry tool; however, such data are rarely acquired. Using a unique dataset from regularly weighed Rothschild giraffes (*Giraffa camelopardalis rothschildi*) from Prague zoo, we determined the growth functions of male and female giraffes and calculated weight gains during giraffe ontogeny. The mean weights of adult males and females were 1307 ± 52 and 835 ± 45 kg, respectively confirming the large overall dimensions of *G. c. rothschildi* in comparison with other giraffe subspecies. As the giraffe is a polygynous species showing considerable sexual dimorphism, we expected male calves to have larger first weights and faster growth during the most intensive period of maternal care. Growth rates and daily weight gains were higher in males than in females during the whole postnatal period. Males grew faster and longer than females. However, differences in weight between males and females appeared as late as after 1 year of age. The weight of adult males and non-pregnant adult females fluctuated significantly across seasons, being the highest during the autumn and winter months, respectively which may reflect the different effects of sexual activity and feeding ratios in males and females. Zoo Biol. XX:XX–XX, 2016.

Keywords: growth function; weight gain; ungulate; *Giraffa camelopardalis rothschildi*; Baringo giraffe

INTRODUCTION

Knowledge of the growth and individual weight fluctuations of endangered species regularly bred in captivity can be a useful tool for both conservation and husbandry purposes. It may allow the assessment of the suitability of a feeding ratio [EEPs, 2006] as well as the social environment in the group [Alados and Escós, 1992]. Information about height and weight at certain ages can also be useful to assess the condition of the animals and detect anomalous growth in newborns, both in captivity and in the wild [Yerga et al., 2014] as well as during hand-rearing [EEPs, 2006], and to estimate weight for immobilization or other medication for animals.

Growth is a physiological process which begins at conception [Robbins and Robbins, 1979] and usually stops at maturity or soon after in most mammals [Kozłowski and Wiegert, 1987]. However, it can continue throughout the whole life [Robbins and Robbins, 1979; Pei, 1996], having important consequences for health, reproduction, and survival [Rodel et al., 2008]. Studies of the size of animals at birth, subsequent postnatal growth, and their characteristics are important for understanding the physiology, behavior, and ecology of animals [Elangovan et al., 2003; Krochmal and Sparks, 2007]. In polygynous species males and females exhibit widely divergent tactics in terms of growth in relation to reproduction, generally leading to marked sexual dimorphism in size [Ralls, 1977; Jarman, 1983]. Sons usually weight more and grow more

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quickly than daughters due to maternal investment [Hewison and Gaillard, 1999], as maternal care differs between sexes in all species which are sexually dimorphic [Kovacs and Lavigne, 1986]. Males usually continue to grow after female growth has stopped [Georgiadis, 1985].

Data about the height and weight of giraffes are highly variable, females 3.5–4.7 m, 450–1180 kg; males 3.9–6 m, 800–1930 kg [Dorst et al., 1972; Hall-Martin, 1976; Estes, 1991; Kingdon, 2003], despite being based on very limited sources originating both from captivity [EEPs, 2006] and the wild [Wilson, 1969; Hall-Martin, 1976, 1977], with little consideration paid to the subspecies of giraffe. Different giraffe taxonomic units (hereafter named subspecies) have been recognized based on distribution range, coloration, and shape of spots, skull dimensions, and molecular ecology [Brown et al., 2007; Hassanin et al., 2007; Groves and Grubb, 2011]. However, it is not mentioned whether the discrepancy in documented giraffe weights could be attributed to subspecies.

There is a general consensus regarding the sexual dimorphism of giraffes in terms of weight; however, information about differentiation in growth patterns between males and females is missing. Bashaw [2003] specified that 2–3-year-old females are 88% the weight of males of the same age and Dagg and Foster [1976] hinted that size dimorphism begins to develop at about 1–2 years of age. The start of size differentiation between the sexes in dimorphic species may be connected with approaching sexual maturity and development of other features as horn growth, gonads development, coat color, and length changes as recorded in mountain goat [Côté et al., 1998], Bulgarian chamois [Massei et al., 1994], common eland, nyala, nile lechwe [Kingdon et al., 2013].

The weight of newborn giraffes recorded in captivity has been reported as between 55 [Dagg, 2014] and 64 kg [Reason and Laird, 2004]. Data for giraffes in the wild are sparse, with weights of 77 and 101 kg at birth reported [Wilson, 1969; Kingdon et al., 2013] and about 1.8 m high, ranging from 1.3 to 2.1 m [EEPs, 2006; Dagg, 2014]. Calves are reported to grow very rapidly during the first months of life, up to 23 cm in height per week [Dagg and Foster, 1976]; however, the mean increase in height has been documented to be about 15 cm per month during the first 6 months, with high inter-individual variability [Dagg and Foster, 1976] and 10 cm per month in Dvůr Králové during the first year of life [EEPs, 2006]. Much of this growth is in the neck region [Backhaus, 1961], as the rate of growth in the neck is similar in both genders and faster than the increase in body mass [Mitchell et al., 2013]. Growth slows down in the 2nd year of age [Dagg and Foster, 1976]. Males grow more quickly than females, reaching their adult height at 4–5 years [Dagg and Foster, 1976]. Hall-Martin [1977] estimated the weight of a giraffe's head and neck region as 250 kg, suggesting that it is considerably lighter than expected due to the existence of several adaptations.

Growth of ungulates is most intensive in calves and, in addition to sex [Lavigueur and Barrette, 1992], it may be influenced by other factors. Some factors can be connected with maternal characteristics, such as the age of the mother [Wright et al., 1975; Eyduran et al., 2008; Aktas et al., 2014], weight of the mother [Kojola, 1993; Birgersson and Ekvall, 1997], and parity [Côté and Festa-Bianchet, 2001; Mandal et al., 2003; Abegaz et al., 2011; Yiheyis et al., 2012]. The effect of heavy females producing heavy offspring has been documented in reindeer [Rognmo et al., 1983; Skogland, 1984], fallow deer [Birgersson and Ekvall, 1997], sheep [Burfening and Carpio, 1993], and cattle [Ali, 2014]. External factors, such as calving season [Yilmaz et al., 2007; Ismail et al., 2011], year of birth [Shahzad et al., 2010; Yilmaz et al., 2013; Hussain et al., 2014], quality of food [Yerga et al., 2014], time spent feeding [Lavigueur and Barrette, 1992], and habitat [Leberg et al., 1992] have also been shown to influence the weight and growth of animals.

The body mass growth pattern in mammals follows a non-linear sigmoidal curve [Zullinger et al., 1984], with a point of inflection at about one-third of the final weight [von Bertalanffy, 1957]. The inflection point of growth, marking its slow-down [Walford, 1946], usually occurs when the young/juveniles start to feed by themselves [Portier et al., 2000; Yerga et al., 2014].

The weight of an individual can also vary in adulthood. In females, the biggest weight gains, as well as the biggest weight losses, are usually connected with pregnancy and parturition [Russel et al., 1968; Thorne et al., 1976] but can also be caused by hormonal changes during estrus [Holand et al., 2005]. Adult males can lose weight during the breeding season [Yoccoz et al., 2002; Mysterud et al., 2003, 2005]. The weight of both males and females can differ according to season and weather, as well as different qualities of feeding ratios [DelGiudice et al., 1992; Festa-Bianchet et al., 1996; Langvatn et al., 1996; Weladji et al., 2002].

The aim of our study was to determine the growth curve of the endangered Rothschild giraffe, a subspecies most frequently bred in European zoos. Regarding the described sexual dimorphism in the giraffe, we aimed to analyze differences in first recorded weight, growth rate and the length of the growth period between males and females. We also analyzed factors connected with weight fluctuations in adult giraffes and assessed the influence of feeding ratios.

MATERIALS AND METHODS

Ethical Note

The weighing of giraffes was carried out regularly during their normal routine by an experienced keepers (including KP) responsible for the animals under the supervision of the head curators (JŠ, BD). The giraffes entered the weighing platform in the corridor while moving into the indoor stables. No specific permissions were required.

Studied Animals

Prague Zoo has a long tradition of Rothschild giraffe breeding and has invested in high quality stables, enclosures, and equipment during the last decades. That is why a unique weighing system TONAVA VT6220 TM3000 (min. 20 kg, max. 3,000 kg, dc. 1 kg) has been installed in the giraffe corridor, enabling regular data collection. The giraffes were trained to walk through the corridor with the weighing platform when returning to the stable from the outdoor exhibit (summer) or from separation boxes (winter) and each individual was individually weighed. Weighing process was individually adapted according to the needs of a specific giraffe.

The animals were kept in a temperate stable during winter months, while they spent most of the days in the outdoor enclosure during the warmer part of the year. They were fed ad libitum with hay and branches, with limited supplements of granulated food, fruit, and vegetables. Females at advanced stages of pregnancy and after parturition were separated and fed milk supplements. During the favorable season (April–October) fresh branches were provided and pasture allowed, and green alfalfa was fed. The green alfalfa was replaced mainly by alfalfa hay during the rest of the year.

For the purposes of this study, we considered a juvenile as a dependent calf under the age of 12 months, a sub adult as between the ages of 1 and 3 years and an adult 4 years or older [EEPs, 2006].

Data Collection

We collected weight data from 43 giraffes from September 2009 until December 2013. For each weight record we noted the date of birth of the animal, its age in months, its sex, its age category (juvenile, sub adult, adult), the weight of the mother, the age of the mother at the date of weighing, the identity of the mother (Kleopatra, Nora, Faraa, Diana, Eliška), the season of birth (spring, summer, autumn, winter), and the season of weighing (spring, summer, autumn, winter). Consequently, we evaluated what we call here the “first weight” of the calf. As the calves could not be weighed on the day of birth, we used the values at the earliest age the calf was weighed. The mean age of calves born during the study period ($n = 12$) at first weighing was 14 days (range 1–25); age did not differ among males and females ($t = -0.05$, df = 10, $P > 0.05$).

Growth Functions

We first used the whole dataset to create the growth curves for giraffes. During the period of data collection, we did not obtain any complete true growth lines (data from an animal from birth to adulthood) as the weighing was performed during a limited time period (4 years). Therefore, we used the mean weights of different individuals at specific ages (0–240 months). We used the CADEMO software to calculate the parameters of the growth functions separately for males and females and to visualize the growth curves. As CADEMO requires no more than 100 points (weights at the specified age) to define the growth function, we used mean weights of females at 0–74 months (0–6 years) at intervals of one month, with a gap between 58 and 65 as data for these ages were missing, and 96–228 months (7–19 years) at intervals of 1 year (77 points in total). For males we used the mean weight every month up to the age of 170 months, with a gap between 29 and 121 months as data for these ages were missing (80 points in total).

CADEMO estimated parameters A, B, and C of the Bertalanffy growth function for males and females separately using the least square method. In addition, the program calculated confidence limits for the parameters, an estimation of the residual variance for a given sample size, within the confidence interval 0.05 (Table 1), and visualized the growth curves (Fig. 1).

$$y = \left(\mathrm{A} + \mathrm{B}e^{\mathrm{C}x}\right)^3$$

We than transformed the Bertalanffy growth function to obtain the asymptotic weight (W_∞), the Bertalanffy weight gain constant (K) and the age at the inflection point (X_0).

$$W(\mathrm{x}) = W_\propto\left(1 - \mathrm{e}^{-K(\mathrm{X}-\mathrm{X0})}\right)^3$$

Data Evaluation

The data were analyzed in Statistica StatSoft. For the first weight of the calves, as for the growth of calves up to 12 months of age, we used a GLM (General Linear Model) with the “identity of the mother” as a random factor. The final model for the first weight of the calf contained identity of the mother (random factor), sex, season of birth, age of mother, and weight of mother.

We calculated values for daily weight gains during the first 12 months, the most intensive growth period, during which the growth pattern was considered linear. We compared the growth ratio, weights, and daily weight gains

TABLE 1. Bertalanffy growth function parameters estimation ($P < 0.05$)

	Male ($s^2 = 1411.5860$)			Female ($s^2 = 918.0580$)		
	Estimate	Minimum	Maximum	Estimate	Minimum	Maximum
A	11.0050	10.9653	11.0448	9.4916	9.4170	9.5663
B	−5.7270	−5.9894	−5.4646	−4.2806	−4.4723	−4.0890
C	−0.0319	−0.0350	−0.0289	−0.0338	−0.0364	−0.0313

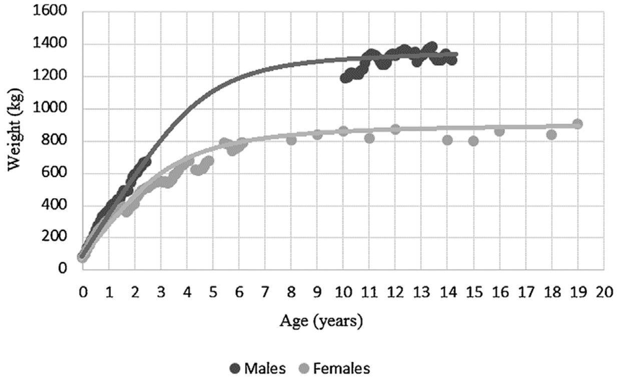

Fig. 1. Bertalanffy growth curves of male and female giraffe.

within the first 12 months between males and females and compared the mean weights of males and females at 0, 3, 6, 9, 12, 15, and 18 months of age using a *t*-test.

We used the known data for parturitions and considering pregnancy to be 460 days [EEPs, 2006], we gave all adult females during specific weighing occasions a value for "month of pregnancy." Data from the nine complete pregnancies which started and finished during the study period were used to create the pregnancy gain chart. We then used those data for further evaluations of pregnancies. The first recorded value in the "month of pregnancy = 1" was used to calculate the mean weight of non-pregnant females. We calculated the mean weight of those females before parturition, using the last weight recorded for a female before her calf was born. From those values we calculated the mean weight gain during pregnancy and the mean daily weight gain during pregnancy. Finally, we compared the difference between mean daily weight gain during the first and second half of pregnancy.

We also used a GLM to assess the influence of age and season on the weight of fully grown non-pregnant females (aged over 96 months). We excluded the oldest female (Berta) from this dataset as she was significantly older and lighter than other females and would violate the weight to age relationship.

We calculated the mean weight of the adult male and analyzed the factors influencing weight changes. We used a GLM to test the influence of age and season on the weight of the adult male.

RESULTS

In total we evaluated 2,184 records of weight from 9 adult giraffes (1 male and 8 females), 15 sub adult giraffes (6 males and 9 females), and 17 calves (6 males and 11 females).

Growth Functions

Parameters A, B, and C of the Bertalanffy growth function were calculated within a confidence interval of 0.05 (Table 1) and the growth curves were visualized for males and females separately (Fig. 1). The asymptotic weight was 1332.82 kg for males and 855.10 kg for females, the Bertalanffy constant was 0.0269 kg/day for males and 0.0208 kg/day for females, and the age at the inflection point was 13.96 months for males and 8.94 months for females.

The First Recorded Weight

Twelve calves were born during the study period, the mean first recorded weight of the calves was 82.33 ± 7.17 kg ($n = 12$, range 71–93 kg). None of the tested factors influenced first weight (age of mother: $F = 0.09$, $P = 0.812$, weight of mother: $F = 14.63$, $P = 0.163$, sex: $F = 9.79$, $P = 0.197$, mother: $F = 6.29$, $P = 0.289$, season of birth: $F = 1.48$, $P = 0.529$).

Growth of Calves

None of the abovementioned factors influenced the weight of the calves at the age of 1 year. However, the growth patterns of males and females during the first year significantly differed ($F = 103.37$, $P < 0.001$), with males increasing in weight more rapidly than females (Fig. 2). The daily weight gain during the first year was significantly higher in males (0.87 ± 0.48 kg, $n = 172$) than in females (0.72 ± 0.43 kg, $n = 307$) ($F = 12.28$, $P < 0.001$), significantly decreasing in females and stable in males (Fig. 3). A significant difference in the mean weight between males and females was recorded in sub adult individuals at the age of 18 months (Table 2).

Adult Females

The mean weight of a female at conception was 808.67 ± 53.91 kg (range 718–903 kg), while the mean weight of a female before parturition was 972.22 ± 40.10 kg

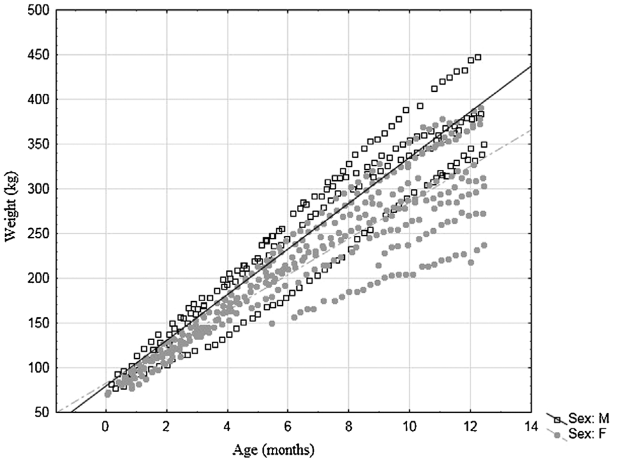

Fig. 2. Detailed visualization of increase in the mean weight of male ($y = 79.9494 + 25.5083x$, $r = 0.9430$, $P < 0.001$) and female ($y = 83.2303 + 20.1725x$, $r = 0.9078$, $P < 0.001$) giraffe calves up to the age of 1 year.

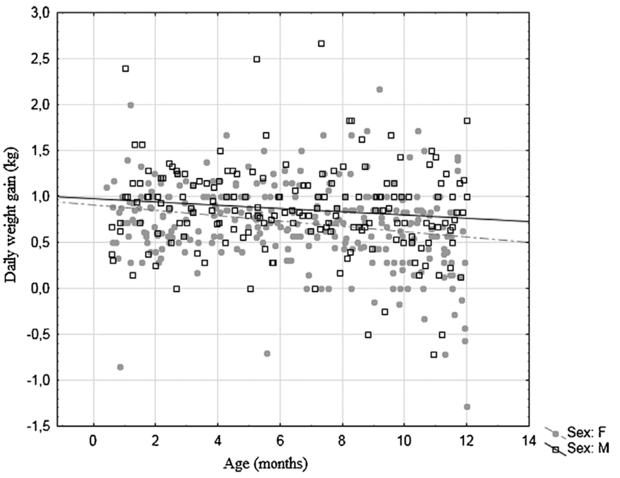

Fig. 3. Daily weigh gain decrease in male ($y = 0.9804–0.0177x$, $r = -0.1245, P > 0.05$) and female ($y = 0.9087–0.0294x$, $r = -0.2314$, $P < 0.001$) giraffe calves up to the age of 1 year.

(range 885–1026 kg) (Fig. 4). The mean weight gain during pregnancy was 163.56 ± 31.25 kg (range 114–222 kg), representing 14–30% of the females' weight at conception. The relative weight-gain during pregnancy significantly decreased in heavier females ($r = -0.78$, $P < 0.05$). The mean daily weight gain during pregnancy was 0.36 ± 0.08 kg and significantly differed in the first half of pregnancy (1st–7th month, 0.148 ± 0.237 kg) and the second half of pregnancy (8th–15th month, 0.548 ± 0.290 kg, $t = -3.02$, df = 14, $P < 0.01$). The mean weight loss after parturition was 111.89 ± 19.95 kg (range 82–150 kg). Neither pregnancy weight gain ($r = -0.18$, $P > 0.05$) nor post-partum weight loss ($r = 0.15$, $P > 0.05$) was related to the first weight of the calf.

The mean weight of a fully grown non-pregnant female was 835.15 ± 45.82 kg (range 740–922 kg). Despite weight fluctuations, the mean weight of females continually increased ($F = 27.44$, $P < 0.01$), and older females were, therefore, heavier. The weight of non-pregnant females was influenced by season ($F = 17.322$, $P < 0.01$), they were heavier during winter (859.92 ± 43.13 kg) and significantly lighter during autumn (807.76 ± 38.73 kg).

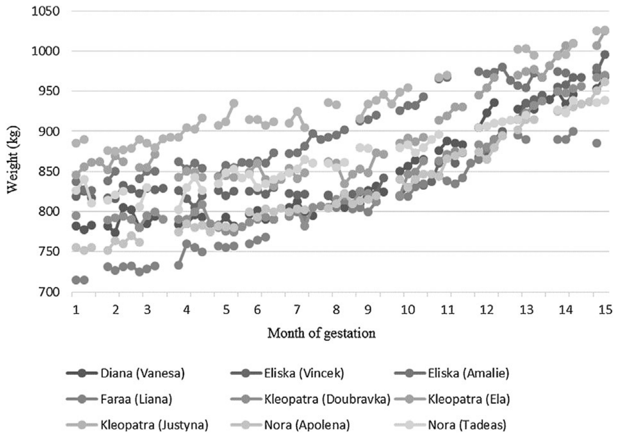

Fig. 4. Weight changes in the five adult females during nine pregnancies. Name of the mother is followed by name of the calf in parentheses.

Adult Male

The mean weight of the only adult male in the studied herd was 1307.77 ± 52.51 kg (range 1182–1391 kg) and was significantly influenced by season ($F = 4.2$, $P < 0.01$), with the highest mean weight recorded in autumn (1327.55 kg) and lowest in summer and spring (1294.37 and 1295.83 kg, respectively). Despite the large fluctuations (Fig. 5), the mean weight of the male continually increased ($F = 149.7$, $P = <0.001$) up until the age of 170 months (the end of the study).

DISCUSSION

Subspecies, Captivity, or Technology?

Our study provides the first detailed and reliable information about the weight of the endangered Rothschild giraffe. The mean weights of our animals were generally 3–8% higher than those reported in other studies [EEPs, 2006; Dagg, 2014]. There are three possible explanations for this discrepancy, none of them mutually exclusive. First, Rothschild giraffes, as a distinct subspecies, may be heavier than other giraffe subspecies. This is supported by the fact that all published weights originate from other subspecies and we, therefore, do not have any comparative data for the

TABLE 2. Differences between mean weights of male and female giraffes, total $n = 18$ (seven males, nine females)

	Males			Females				
Age (months)	n	Mean weight ± SD (kg)	Range (min–max)	n	Mean weight ± SD (kg)	Range (min–max)	t-test (df)	P
0	4	86.25 ± 8.06	77–93	8	80.38 ± 6.32	71–90	1.39 (10)	0.194
3	4	147.00 ± 22.46	115–167	7	137.14 ± 8.67	127–153	1.064 (9)	0.315
6	4	238.00 ± 41.09	179–273	8	207.00 ± 25.66	158–242	−1.62 (10)	0.134
9	4	320.75 ± 31.94	270–356	9	267.78 ± 40.73	195–328	−2.12 (11)	0.057
12	5	376.80 ± 43.59	332–444	8	316.75 ± 55.80	218–375	2.037 (11)	0.066
15	5	416.80 ± 50.99	357–496	8	360.88 ± 54.77	268–422	1.836 (11)	0.093
18	6	478.00 ± 43.90	405–542	7	385.86 ± 59.56	299–473	2.785 (11)	0.018

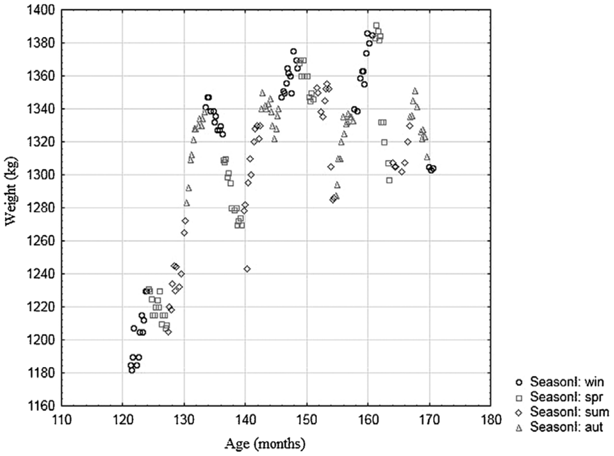

Fig. 5. Weight changes in the adult male Johan during different seasons of the year.

Rothschild giraffe, either from the wild or in captivity. Moreover, while assessing giraffe morphology, Groves and Grubb [2011] reported a remarkable morphocline extending from the smaller Southern giraffe taxa to the larger Northern ones. In their study, the *camelopardalis* taxonomic unit falling in the northern taxa includes the *rothschildi* specimens and shows considerably larger skull dimensions than other giraffe taxa, suggesting that the Rothschild giraffe belongs to the largest and, therefore, heaviest giraffe subspecies [Groves and Grubb, 2011]. Secondly, the larger body mass of our giraffes may be an artefact of captivity, for example, high quality nutrition [Kimura and Hamada, 1996; Crossley and del Mar Miguélez, 2001; O'Regan and Kitchener, 2005], in combination with a limited physical activity, especially during winter when access to the outdoor enclosure is restricted. This explanation is supported by the fact that the adult non-pregnant females in our study were significantly heavier during winter. However, the weights of captive giraffes from other subspecies are lower than those obtained in our study, which favors the previous explanation. The third explanation is connected to the origins of other published references on giraffe weight. We cannot exclude the possibility that the higher weights in our sample may have been obtained just due to better technology and a more controlled approach to weighing.

Giraffe Growth—the Weight and Height Relationship in the Context of Sexual Dimorphism

The mean first weight (during the first 2 weeks of life) of the calves in our study was slightly higher than weights of newborn giraffes from other studies in captivity, which ranged from 51 to 81 kg. This fits with the overall higher weights reported in our study. We did not find a significant difference between the first weights of males and females; however, males tended to be heavier.

Our results confirmed the observations of Dagg and Foster [1976], who stated, based on height measurements, that males grow faster and that size dimorphism in giraffes begins to develop at about 1–2 years of age. In our study, males grew faster and a significant difference between males and females in terms of weight appeared between 15 and 18 months of age. The weight difference appears in the period when males enter puberty and the period of sexual maturity starts [Festa-Bianchet et al., 1996], which corresponds with the development of secondary sexual dimorphism in other ungulate species [Massei et al., 1994; Côté et al., 1998; Kingdon et al., 2013]. The age at the point of inflection was considerably higher in males than in females, showing longer and more intensive growth in males in the postnatal period. Our findings correspond with the described neck mass growth, which is reported to increase with age in both sexes. Female neck growth of wild giraffes stops at about 10 years of age, while males continue to allocate linearly in larger necks as they age [Simmons and Scheepers, 1996]. Despite the specific proportions of giraffes, the weight of the giraffe's long neck and its head is surprisingly low, and the rate of increase in neck length is similar until puberty in both genders [Mitchell et al., 2013], with growth in height corresponding with increasing body mass. Both sexes increased their weight also in adulthood.

Generally in dimorphic polygynous species, sexual dimorphism is characterized by higher weight and postnatal growth rate in males compared to females [Lee and Moss, 1986]. In many species, body size can strongly influence the reproductive success and survival of a male [McElligott et al., 2001; Preston et al., 2003]. In giraffes, larger males exhibit proportionately larger necks and heads, which are used both in intrasexual aggression and for gaining access to estrous females [Simmons and Scheepers, 1996]. In addition, bigger and especially taller males are more successful in feeding competition, being able to browse at the upper level of the canopy [Ginnett and Demment, 1999]. This positive correlation between body size and reproductive success in males may have led to differential maternal investment in offspring [Trivers and Willard, 1973].

The growth pattern which we reported highlights the importance of the nursing period for the pronounced growth of male offspring. Several studies have suggested that mothers invest more in male offspring through higher birth mass, provisions of more milk or later weaning, which leads to faster growth [Lee and Moss, 1986; Wolff, 1988; Birgersson and Ekvall, 1997; Landete-Castillejos et al., 2004]. Differences in the condition of young at the end of the period of maternal investment may endure into adulthood [Trivers and Willard, 1973]. Growth rates could be positively correlated with suckling rate in calves [Lavigueur and Barrette, 1992]; however, differences in maternal investment in males and females in the form of nursing were not found in giraffe [Gloneková et al., 2016]. Our findings therefore suggest that as the significant difference between the male and female weights appears at the time of weaning (15–18 months), the intake of solid food may play more important role for the growth rates.

Feeding or Sex? The Influence of Season on Giraffe Weight

Of all the external factors tested only season influenced the weight of adult animals, but not the weight of calves. Moreover, the results differed for the breeding male, which was significantly heavier during the autumn and summer months, and for non-pregnant adult females, which were heavier during the winter. The feeding ratio and husbandry system in our study differed between summer and winter. The winter feeding ratio contained alfalfa hay, which is rich in nutrients, and access to the outdoor enclosure was restricted, suggesting that the giraffes moved less than during the summer months. This may be reflected in the weight increase in females during the winter months. Wild giraffes lose condition as the quality of their diet declines during the dry season [Hall-Martin, 1976]. As predicted [Russel et al., 1968; Thorne et al., 1976; Hewison and Gaillard, 1999], the weight of adult females was mostly affected by pregnancy. The first weight of a calf made up in average 54% of the weight gain during pregnancy and was highly variable (37–81%). While older females tended to be heavier, they apparently gained proportionally less weight during pregnancy than the younger females. However, our sample is rather small to make any general conclusions.

The weight changes in the only adult male should be interpreted with caution, as they may reflect specific features of an individual rather than a general situation. However, we can discuss why the weight changes in the male did not reflect the changes in the feeding ratio and husbandry in the same way as they did in females. Given that eight out of the 12 births of calves that occurred during our study occurred between January and June, and that giraffe females come into estrus usually 2 months after parturition, the weight changes in the male may reflect its interest in females in estrus, which occurs mainly during the spring and summer months. A similar pattern of seasonal weight loss was reported in moose [Franzmann et al., 1978] and in other ungulates [Mitchell et al., 1976; Deutsch et al., 1990; Yoccoz et al., 2002; Mysterud et al., 2003; Mysterud et al., 2005]. Estrus may also influence the weight of females, as reported in reindeer where females lose body mass [Holand et al., 2005]; however, we did not have detailed information about estrus in specific females to assess these changes.

In contrast with adults, season did not affect the first weight of calves. We expected that the weight of calves would reflect either the season [Yilmaz et al., 2007; Ismail et al., 2011] or the weight of the mother, due to the accessibility of resources both for the calf and for the female. Giraffe breeding is not driven by seasonality in most localities, but we might expect that in areas with strong differences between dry and rainy seasons an influence would appear. Although in some ungulates, older mothers produce heavier offspring than younger females [Wright et al., 1975; Wilson, 1987; Duguma et al., 2002; Matika et al., 2003] we did not find any effect of maternal age on the body mass of calves. Similar results were reported in mountain goats [Côté and Festa-Bianchet, 2001]. It is also possible that a more important factor than age is the parity of the mother. We could not evaluate the influence of parity in our study as only one primiparous female was included. The absence of an influence of internal factors on calf first weight, weight of the mother, and age of the mother, may be explained by our low sample size and the generally stable conditions in captivity, where energy intake does not represent the limiting factor. The kinds of trade-offs that are made with respect to parental investment (e.g., males vs. females) may therefore not be relevant.

CONCLUSIONS

The Rothschild giraffe may belong to the heaviest giraffe subspecies in accordance with its larger skull dimensions. Sexual dimorphism with respect to giraffe weight develops gradually through the postnatal period, showing higher postnatal weight gains in male compared to female calves. The significant difference between the weight of males and females appears at 18 months of age. In addition to this, males continue to increase their weight longer than females. Season influences the weight of adult giraffes, most likely reflecting the husbandry system and feeding in females and sexual activity in males.

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5.4. Giraffe nursing behaviour reflects environmental conditions

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Giraffe nursing behaviour reflects environmental conditions

Short title: Influence of environment on giraffe nursing

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ABSTRACT

Nursing behaviour is one component of a mammalian life history strategy that demonstrates context-dependent flexibility within species. Wild giraffes live in groups where individuals are often far apart, and their calves are mostly considered “hiders”. In the zoo, giraffes are kept in enclosures with limited space, abundant food resources and without predators. Allonursing was reported mostly from captivity and explained by milk-theft and reciprocity in giraffes. We aimed to analyse which factor (food intake, presence of predators, population density) can explain the difference in nursing behaviour of giraffes between the two environments. We observed seven and four female-calf pairs in a fenced Bandia reserve, Senegal, and in the Prague zoo, Czech Republic, respectively. Nursing bouts, which were less frequent and longer in the reserve, were likely to reflect anti-predator behaviour and the distribution of food resources. Calves in the zoo were more successful in nursing solicitations, as females in the reserve were more selective for nursing times and locations, either due to food intake or presence of predators. Allonursing occurred more frequently in the zoo which can be attributed by higher population density and unlimited food intake there.

Key words: *Giraffa camelopardalis*, nursing, suckling, allonursing, milk-theft, hider

1. Introduction

Wild and captive behavioural comparisons provide opportunities to assess the influence of proximate factors, helping to understand the behavioural plasticity of species (Komers, 1997). This is especially interesting in the case of nursing behaviour belonging among the most energetically costly parts of parental investment (Clutton-Brock, 1991), and requiring well-balanced trade-offs in terms of resource partitioning. From an evolutionary point of view, a species' life history and specific adaptations influence the suckling behaviour (Ralls et al., 1987). These ultimate factors, in response to the availability of resources and presence of predators, formed the "hiding" or "following" rearing strategies, which influence nursing frequency and duration (Lent, 1974). "Hiding" calves are only nursed a few times a day with longer suckling bouts, as in roe deer, *Capreolus capreolus*, nursing for 20 – 40 min (Rosenblatt et al., 1985), while "following" calves may suckle more often with shorter bouts, as in caribou, *Rangifer tarandus*, nursing 50 s only, 30 times per day (Parker et al., 1990).

The general nursing pattern is influenced by proximate factors, which comprise current social and environmental conditions. These conditions differ considerably between wild and captive populations, and include food intake, presence of predators and actual population density (Therrien et al., 2008).

Animals face decisions on how to allocate all activities to ensure their survival and fitness (Illius et al., 2002). Optimal time allocation for foraging behaviour may be constrained by many factors, forcing animals to adopt compromises to meet their daily energetic needs (Hamel & Côté, 2008). Wild ungulates, including giraffes, spend quite a large part of the day feeding themselves (Pellew, 1984a, 1984b). Adult giraffes spend approximately half of the 24-hour-day feeding (Pellew, 1984a).

To compensate for high energy expenditures, lactating females are expected to modify their foraging behaviour to increase nutrient intake (Hanwell & Peaker, 1977; Bunnell & Gillingham, 1985; Ruckstuhl & Festa-Bianchet, 1998), which can be achieved by foraging even longer (Shipley et al., 1994). However, lactating females face a fundamental trade-off between foraging, vigilance (Illius & Fitzgibbon, 1994; Cowlishaw et al., 2004) and nursing (Rachlow & Bowyer, 1998; Toïgo, 1999; Hamel & Côté, 2008; Pluháček et al., 2010). High population density may help individuals to decrease time spent on vigilance, however it also belong to one of the factors explaining existence of allonursing, nursing of non-filial offspring (Packer et al., 1992). Under high population densities, so called “milk-theft” belongs among the most represented hypotheses explaining allonursing, usually connected with suckling in parallel position which prevent calf’s identification by the nursing female (Brandlová et al. 2013; Gloneková et al., 2016).

Giraffe calves have been described both as “followers” (Kitchen, 1977; Horwich et al., 1983) and “hiders” (Langman, 1977). Ralls et al. (1986) ranked the giraffe in an “intermediate” cluster, suggesting their ability to react to changing environmental conditions. The nursing duration in giraffes is highly variable (4 s to 360 s; Langman, 1977; Pratt and Anderson, 1979; Nakamichi et al., 2015) and the reason for this is unknown. Giraffe calves are born year round (Bercovitch & Berry, 2010). Females typically give birth to one calf and rarely have twins (Foster & Dagg, 1972). Wild females leave the herd before parturition and usually give birth alone (Estes, 1991). A week or two after parturition, the calf mostly hides and the mother feeds apart, with nursing occurring several times a day (Langman, 1977). Later the mother and calf join other females with offspring (Pratt & Anderson, 1979). Calves of similar age form nurseries, guarded by one female, while the other mothers are feeding (Pratt & Anderson, 1979). Giraffe mothers in Bandia reserve spent more than 60% of time accompanied by the filial calf (Malyjurková et al., 2014).

Captive giraffes are also typically separated before parturition and give birth alone (EAZA Giraffe EEPs, 2006). The time when they return to the herd depends on husbandry management decisions. Nurseries are less obvious as the space is limited, food provided, and females are constantly associated with the calf (Greene et al., 2006). In captivity, the time spent feeding is shorter (Veasey et al., 1996), and the feeding pattern is markedly changed (Baxter & Plowman, 2001). Allonursing was recorded in giraffes more frequently in captivity (Gloneková et al., 2016) than in the wild (Pratt & Anderson, 1979). This pattern of allonursing occurrence corresponds with other "hiders", such as the common eland *Taurotragus oryx* (Hejcmanová et al., 2011) and species with an "intermediate" strategy such as the camel *Camelus bactrianus* (Brandlová et al., 2013). Explanations for allonursing in giraffes are variable, oscillating between reciprocal help among females sharing nursing duties in nurseries and the milk-theft theory (Gloneková et al., 2016).

We aimed to examine the differences in nursing behaviour of giraffes in the reserve and in the zoo in an attempt to assess the plasticity of giraffe nursing behaviour with specific regard to food intake, presence of predators and population density. We assumed that if food intake is the factor influencing nursing behaviour than the rejection of nursing will be more frequent in the reserve than in captivity, as captive giraffes have ad libitum food intake. We further assumed that the difference in nursing behaviour is caused by the presence of predators. In this case giraffes in the reserve nurse less frequent and longer than the giraffes in the zoo, and females in the reserve are more vigilant, meaning that they observe their surroundings while nursing and are selective for nursing times and locations. The last we suppose the influence of current population density will lead to lower vigilance in the zoo than in the reserve but will be connected with more opportunities for allonursing.

2. Materials and methods

2.1. Study area

In Senegal, introduced Cape giraffes (*Giraffa camelopardalis giraffa*) were observed in the Bandia reserve, a fenced area run for the purpose of safari-tourism which contributes to the protection of the environment and wildlife conservation at the same time. Encompassing an area of approximately 3500 ha, the reserve was created on the southwest boundary of the ‘Classified Forest Bandia’ by the Society for Protection of Environment and Fauna in Senegal (SPEFS) in 1990 (Nežerková et al., 2004). Based on phytogeography, the reserve belongs to the Sudan-Sahelian area (Antonínová et al., 2004). The landscape is formed by plains with baobabs and dense shrubs that make animal observation difficult. The original vegetation is composed of a variety of acacia species (Hejcmanová et al., 2010), primarily *Acacia seyal* (Antonínová et al., 2004), which are the main nutrition source for giraffes. Two distinguished seasons characterise the climate: the dry season (from November to June) and the rainy season (from July to October) (White, 1983; Lawesson, 1995). Fauna in the Bandia reserve encompasses originally Senegalese species, such as African buffalo (*Syncerus caffer brachyceros*), roan antelope (*Hippotragus equinus koba*) and Western Derby eland (*Taurotragus derbianus derbianus*), as well as animals introduced from South Africa, as common eland (*Taurotragus oryx oryx*), impala (*Aepyceros melampus*), greater kudu (*Tragelaphus strepsiceros*), and giraffes (*Giraffa camelopardalis giraffe*) (Al-Ogoumrabe, 2002). Predators are represented by golden jackal (*Canis aureus*), and spotted hyenas (*Crocuta crocuta*) which may incidentally enter the reserve.

A captive herd of Rothschild's giraffes (*Giraffa camelopardalis rothschildi*) was observed in the Prague Zoo, where all giraffes were kept in a temperate stable during most of the winter months. The giraffes spent most warm days in outdoor enclosure (2 ha), sharing the space with other species including common eland (*Taurotragus oryx spp*.), addax (*Adax nasomaculatus*), beisa oryx (*Oryx beisa*), red lechwe (*Kobus leche cafuensis*) and Grevy's zebra (*Equus grevyi*). Giraffes were fed *ad libitum* with alfalfa hay and with limited amounts of branches and supplements of granulated food, fruit, and vegetables.

2.2. Studied animals

In the Bandia reserve, seven females with one calf each from a total of 28 giraffes present in the reserve, whose ancestors were introduced from South Africa in 1997, were observed during the dry season. The spacious area of the reserve enables giraffes to behave naturally, thus breeding occurs non-seasonally, females leave the herd for parturition and births occur without human intervention. Following the reserve's requirements, all observations were conducted from a vehicle. During the first week of observations, each individual was identified according to the unique skin pattern, body size, shape of the horns, shape of the hooves, and sex (Estes, 1991). Photographs of each giraffe were taken from both sides, and ID cards were created to facilitate the identification. Mother-calf dyads were identified by maternal behaviour, particularly nursing.

In Prague zoo, we observed four females with one calf each (from a total of 13 giraffes present in the enclosure). Females at advanced stages of pregnancy, during parturition and shortly after parturition were separated and fed with milk supplements. All calves in the herd were sired by the same bull, making them half-siblings to one another. Giraffes were identified individually as above.

For our study, giraffes were considered calves up to the age of about 18 months, when they generally stop suckling and leave their mother (Pellew, 1984a). Calves of various ages were present in both types of environments. While in the zoo exact data of calf ages were known, in the reserve we were unable to determine that, we only divided them into smaller ones and bigger ones for better orientation (Table 1).

Table 1.

The overview of observed calves in the two environments.

Name	Environment	Sex	Age (months)	Age category
Doubravka	Zoo	F	1 – 9	
Frantisek	Zoo	M	3 – 12	
Kuba	Zoo	M	5 – 12	
Vilma	Zoo	F	0 – 9	
Bertik	Nature reserve	M		Smaller
Dusan	Nature reserve	M		Bigger
Lenka	Nature reserve	F		Smaller
Majda	Nature reserve	F		Smaller
Marketa	Nature reserve	F		Bigger
Ruzenka	Nature reserve	F		Smaller
Vilem	Nature reserve	M		Bigger

2.3. Data collection

In Senegal, the data were recorded between 10th January and 13th March 2013. Due to climatic conditions, data collection was generally conducted during two sampling periods each day. The morning period started at 08:00 h, with a break at noon starting at 12:00 h corresponding to the temperature peak, and the afternoon sampling period started at 15:00 h and continued until dusk. In the zoo, the observations were conducted every 14 days between January and October 2011. Each sampling period lasted for 6 h. During the sampling period, all visible suckling solicitations were recorded *ad libitum.*

A suckling solicitation included either suckling attempt or successful nursing bout. A suckling attempt was defined as the act when the calf took the teat into the mouth for less than 5 s (Drábková et al., 2008), or when the calf just approached the udder of the female closer than the length of the head of the calf (Špinka & Illmann, 1992). For the definition of nursing bout, we followed Drábková et al. (2008), who described it as each situation when the calf held the teat in the mouth for 5 s or longer, irrespective of the number of calves simultaneously participating in one nursing. The nursing bout was considered finished when the calf stopped suckling for more than 10 s (Drábková et al., 2008).

For each solicitation, we recorded identity of the nursing female, identity of the suckling calf, position (antiparallel, parallel, perpendicular (Bartoš et al., 2001; Zapata et al., 2009; Fig. 1), initiation (female/calf), relationship between the suckling calf and nursing female (filial/non-filial), identification of the calf by female using sniffing, licking or nosing (yes/no), nursing duration (in seconds), activity of female (feeding/watching surroundings), and environment (zoo/reserve). It should be noted that the antiparallel and perpendicular positions are thought to enable the lactating female to identify the calf (Packer et al., 1992; Bartoš et al., 2001; Brandlová et al., 2013), while the parallel position does not allow the female to recognise the calf (Bartoš et al., 2001; Brandlová et al., 2013; Zapata et al., 2009).

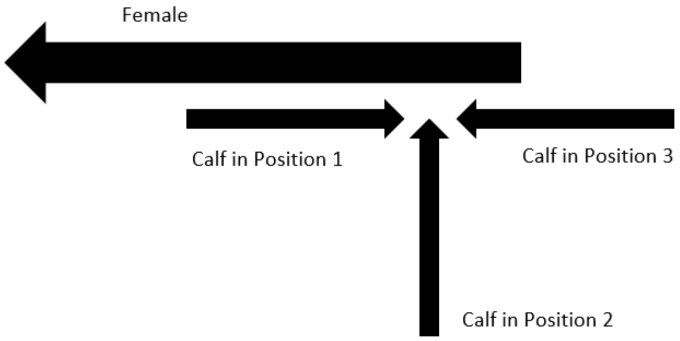

Fig. 1: The schema of nursing positions (1 = antiparallel position; 2 = perpendicular position; 3 = parallel position). Direction of the arrow indicate the head of animal.

2.4. Data analyses

The data were analysed with the STATISTICA 12 software package (StatSoft Inc., Tulsa, OK, USA, 2013). As the data were not normally distributed, we used non-parametric tests. First we calculated the suckling success for each female-calf pair (number of nursing bouts/total number of solicitations) to assess the rejection rates of nursing. We used the Mann-Whitney U test to compare two groups of variables, specifically nursing duration and suckling success according to activity of the female, relationship, sex, initiation and identification. We analysed those values for both environments separately and then we focused on the difference between the two environments (reserve, zoo). We used contingency tables to assess the relationship between categorical variables (position/environment).

3. Results

In the nature reserve, we recorded in total 141 solicitations during 22 days, and 10 of the solicitations included a non-filial calf (7.1%). Solicitations resulted in 13 nursing bouts (9.2%), and none of the nursing bouts were non-filial. The mean nursing bout duration was 47.3 ± 12.6 s (range 25-67 s).

In the zoo, we recorded 574 solicitations during 22 days, and 118 of the solicitations included a non-filial calf (20.6%). Solicitations resulted in 120 nursing bouts (20.9%), of which 28 included non-filial calf (23.7% of all nursing bouts). The mean nursing bout duration was 20.25 ± 17 s (range 5-67 s).

The nursing bout duration did not differ according to the sex of the calf ($U = 1750.00$, $Z = 1.12$, $p = 0.24$) nor according to the age of the calf in the zoo (Spearman $r = -0.094$, $p > 0.05$). The mean nursing duration was significantly longer in the reserve ($U = 209$, $Z = 4.65$, $p < 0.001$; Fig. 2). Regarding the number of suckling solicitations needed for a nursing bout, the calves were more successful in the zoo than in the reserve ($U = 154.5$, $Z = -2.11$, $p = 0.021$, Fig. 3), resulting in a lower suckling success in the reserve. Calves in both environments were more successful when females were observing their surroundings and therefore not feeding themselves ($U = 28$, $Z = 2.1$, $p = 0.036$). The nursing bout was also longer in both environments when females were not feeding themselves ($U = 1251$, $Z = -6.41$, $p < 0.001$), however there was only one episode in the reserve where the female was feeding herself while nursing. The nursing bout was also longer when initiated by the female in both environments ($U = 999.5$, $Z = -2.478$, $p < 0.05$), but a female initiated nursing only once in the reserve with the rest initiated by the calf. Solicitations in both environments were mostly unsuccessful when calves adopted parallel positions, while nursing bouts were more likely to occur in antiparallel (zoo) and perpendicular (reserve) positions. Nursing in the zoo was longer when the calf suckled in antiparallel or perpendicular position than in the parallel position (U = 1046, Z = 2.392, p = 0.0167). Calves in the reserve never suckled successfully in the parallel position (Fig. 4).

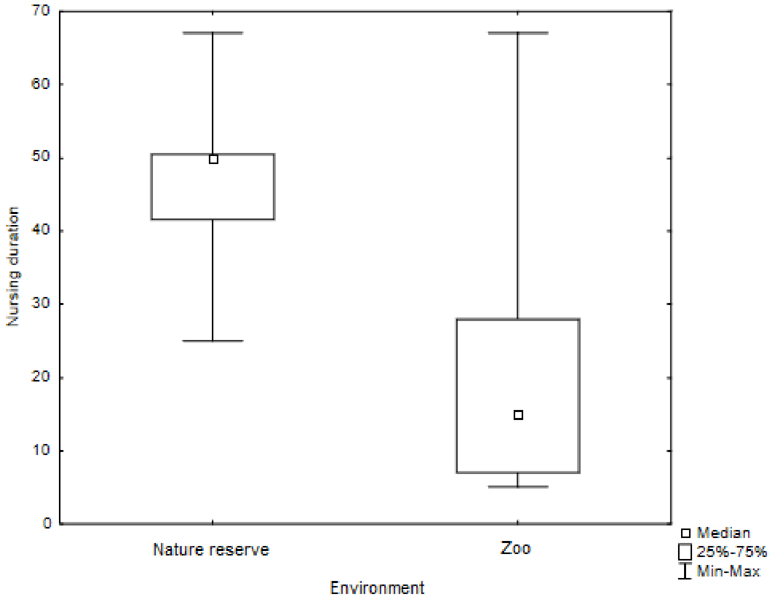

Fig. 2: The difference in nursing duration between two different environments.

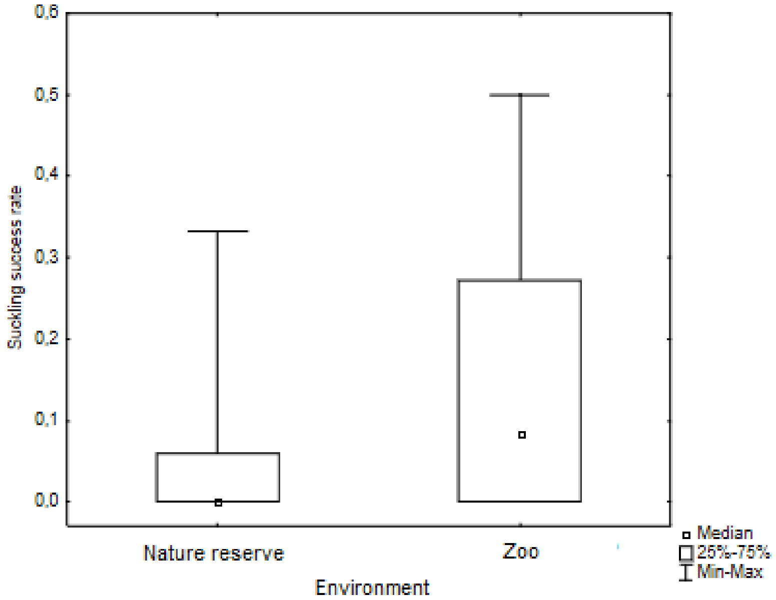

Fig. 3: The difference in suckling success proportion of the calves between two different environments.

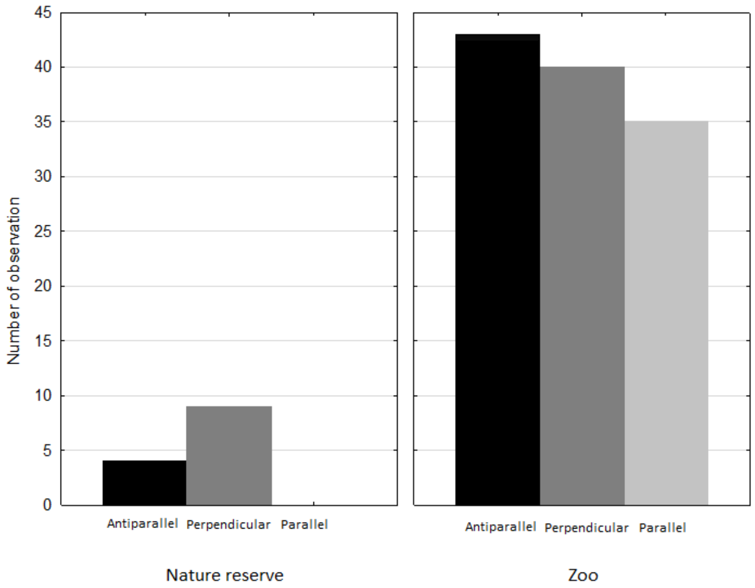

Fig. 4: The difference in suckling position of the calf between the two environments.

4. Discussion

This study compared the nursing behaviour of giraffes in two different environments, a zoological garden and a fenced reserve. The data for this study were collected by the same observer using the same methodology in both environments what makes the study unique. We recorded significantly fewer suckling bouts in the reserve than in the zoo during the same amount of time, as giraffes in the reserve are not forced to stay within view of the observer and recording is limited by dense vegetation where even the tall giraffe may easily remain undetected. Despite this, we revealed significant differences between general nursing patterns in the reserve and in the zoo. Our results suggest that the nursing behaviour reflected differences in the food intake, presence of predators (reflected by vigilance) and population density in respective environments and confirmed a high behavioural plasticity of giraffes (Komers, 1997; Horová et al., 2015).

In the reserve, nursing bouts were more often initiated by calves, and a female initiated nursing in only one case. In the zoo, females initiated 23.7% of nursing bouts. Nursing bouts initiated by females were longer than those initiated by calves. However, the nursing initiation looked different in the reserve compared to the zoo. Calves in the zoo successfully initiated suckling regardless of the activity of the mother and with little impact of the position they adopted. However, in the reserve, calves approached mothers and successfully initiated suckling only when the mother stood still and observed surroundings, appearing as though she was waiting for the calf and not devoted to any other activity. The initiation in the reserve was typical for “hiding” calves and could therefore be understood as mutual, similar to that described by Pratt & Anderson (1979).

Calves in the reserve needed more solicitations for one nursing bout than calves in the zoo. The lower suckling success rate in the reserve was likely connected with a higher need for the mother's vigilance in natural conditions, as the mother's vigilance may directly contribute to offspring survival (Lima & Dill, 1990; Hunter & Skinner, 1998). Females in the reserve seemed to reject the suckling solicitations of calves until they felt safe, observed their surroundings and use the window of opportunity with no predators or other disturbing factors. This may include also the presence of the observer, despite the fact that the giraffes in the reserve are habituated to the presence of cars.

The difference in nursing duration was striking, as nursing duration in the reserve was almost twice as long as in the zoo. Longer nursing in the reserve may be connected with lower nursing frequency and explained both by differences in food intake or by vigilant behaviour. Mean mother-calf distance in the reserve is larger than in the zoo, as in the reserve the female searched for food and often left the calf alone (Malyjurkova et al., 2014), suggesting that calves in the reserve have fewer opportunities for nursing solicitations than calves in the zoo, which may result in an overall lower nursing frequency. Due to longer intervals between nursing bouts, more milk may be accumulated in the giraffe udder in the reserve and the calf may take longer to empty it. Moreover, we can expect that females in the reserve choose the right time and location to nurse their calves to minimise the risk of predation. Consequently, when they find a proper/secure time and place they may try to take advantage of it which results in longer nursing durations. Our finding corresponds with other studies describing longer nursing durations in the wild. Langman (1977) measured the nursing duration of giraffes to be 45-360 s, and Pratt and Anderson (1979) measured the mean nursing duration as 66 s, with 57 out of 415 nursing bouts taking more than 120 s. Nakamichi et al., 2015 observed approximately 60 s long nursing duration or less in captive giraffes when the young became one month old. Significantly longer nursing bouts in the wild compared to captivity were also reported in other ungulates such as camels (Brandlová et al., 2013) and goats (Bungo et al., 1998).

In the reserve, the trade-offs between food intake and vigilance apparently resulted in different nursing patterns than in the zoo. Despite a longer time spent feeding in the reserve, the giraffes almost never fed themselves during nursing, while feeding during nursing was relatively common in the zoo. This was likely due to higher vigilance in the reserve where the giraffes always carefully watched their surrounding during nursing to search for predators. Calves were more successful (their solicitations were less likely to be rejected) when females observed their surroundings instead of feeding themselves both in the reserve and in the zoo, and such nursing bouts were also longer. We recorded only one case when a calf succeeded in suckling solicitation while the female was feeding herself in the reserve, while in the zoo the calves often initiated nursing bouts even if the females were feeding themselves.

We also recorded differences in the suckling position of the calf. While calves were mostly unsuccessful in suckling solicitations when standing in the parallel position in both environments, as in

Brandlová et al. (2013), the position of calves during nursing bouts differed. Calves in the reserve suckled mostly in the perpendicular position and less suckling occurred in the antiparallel position, while the parallel position was never used for suckling. Calves in the zoo suckled most often in the antiparallel position, but often also in the perpendicular and parallel positions. The parallel position makes the identification of the calf for the female harder (Packer et al., 1992). Nursing in the parallel position was also shorter. These results suggest that females in the reserve were more focused on identification of calves during nursing which may prevent non-filial calves from allonursing if explained by milk-theft (Gloneková et al., 2016). We explain those differences by different population densities in respective environments. Higher population density in the zoo can probably explain also the fact that in this study, 23.7% of nursing in the zoo was allonursing, while in the reserve we only found allonursing attempts. Allonursing in wild giraffes has been incidentally documented (Dagg, 1971; Pratt and Anderson, 1979), while Gloneková et al. (2016) recorded the highest allonursing rate among non-domesticated mammals in captive giraffes with more than 80% of females allonursing. Several hypotheses explaining allonursing in captive giraffes were described in detail by Gloneková et al. (2016). The results from that study favoured the milk theft hypothesis, when the offspring allosuckle from a nonmaternal female in a position where it is hard for the female to identify or even refuse the calf, i.e. from the parallel position (Packer et al., 1992). In our study, calves in both environments attempted to suckle and to allosuckle in the parallel position, but only in the zoo did calves in this position succeed and suckle. Such behaviour could be supported by lower vigilance of zoo females, which were less concentrated on identification of suckling calves. Long inter-individual distances and unlimited space enable lactating females to select a remote place for nursing, which in combination with careful identification of the suckling calf decreases opportunities for milk-theft. Allonursing in wild giraffes (as documented by Pratt and Anderson (1979) and others) could therefore be explained by an adaptive hypothesis.

4.1. Conclusions

Nursing bouts were less frequent in the reserve than in the zoo, but with longer duration, which reflects anti-predator behaviour and distribution of food resources connected with the hiding strategy. Females in the reserve observed their surroundings while nursing their calves, and while the zoo giraffes often fed themselves during nursing those nursing bouts were more frequent and shorter. Calves in the zoo were more successful in nursing solicitations than calves in the reserve, as females in the reserve needed to be vigilant and selective for nursing times and locations.

Females in the reserve always nursed in the positions which allowed identification of calves, while this was not the case in the zoo where calves sometimes suckled in the parallel position which prevented their recognition. Finally, allonursing (nursing of non-filial calves) occurred more frequently in the zoo than in the reserve. Nursing behaviour of giraffes in the reserve was more conscious and provided fewer opportunities for milk-theft.

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5.5. Social Preferences of Translocated Giraffes *(Giraffa camelopardalis giraffa)* in Senegal: Evidence for Friendship among Females?

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Original Research Articles

Social Preferences of Translocated Giraffes (*Giraffa camelopardalis giraffa*) in Senegal: Evidence for Friendship among Females?

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Abstract

Giraffe social behaviour and relationships are currently in the period of scientific renaissance, changing the former ideas of non-existing social bonds into understanding of complex social structures of giraffe herds. Different giraffe subspecies have been studied in the wild and only one was subject of detailed study in captivity. Our study focused on the neglected Cape giraffe (*Giraffa camelopardalis giraffa*). We investigated the social preferences of 28 introduced giraffes in semi-captivity in Bandia reserve, Senegal. Our aim was to assess the group size of Cape giraffes outside their native range and describe their social relationships. Mean group size in Bandia was 7.22 ± 4.06 (range 2-17). The dyads were classified according to strength of relationship (weak, medium, strong) using the association index. We reported weak and medium relationships in all types of dyads except female-juvenile. The strongest bond was found in mother-calf dyads. Three of 21 possible female dyads also demonstrated strong relationships. Those three dyads included six of seven adult females, which we labelled as friends. Females associated more frequently with calves of their friends then with calves of non-friend females. The strength of the relationship between calves depended on the strength of relationship between their mothers. We concluded that Cape giraffes in new environment have shown similar group size and non-random preference for conspecifics as shown in wild and captive studies. The research was supported by CIGA 20135010, CIGA 2134217, IGA FTZ 20135123, ESF/MŠMT CZ.1.07/2.3.00/30.0040.

Keywords: *Giraffa camelopardalis*; translocation; female; calf; social bond; fission-fusion system; relationship; friendship; association index.

INTRODUCTION

A giraffe herd is described as individuals that are generally engaged in the same activity such as foraging, drinking, resting, and moving in a coordinated manner in the same direction (Bercovitch and Berry, 2010; Le Pendu et al., 2000; Shorrocks and Croft, 2009). Interindividual distances are often long and giraffes in such a herd may be 1 km apart (Estes, 1991). We use the term "group" for all giraffes within the sight of an observer.

Previous studies concluded that giraffes were associated randomly. They were described as forming only loose, unstable and frequently changing ties to their conspecifics (Estes, 1991; Le Pendu et al., 2000). The only strong bond among giraffes was described between a mother and her dependent calf (Langman, 1977) and between young giraffes (Le Pendu et al., 2000). In small herds strong associations developed among adult females (Fennessy, 2009). Recent studies reported that female giraffes showed significant preference for, or avoidance of, other giraffes (Bercovitch and Berry, 2012). In the wild, female giraffes form a stable population of individuals that is divided into geographically distinct subgroups, despite the absence of physical barriers (Carter et al., 2013b; van der Jeugd and Prins, 2000). Giraffe males are aggregated to bachelor groups or remain solitary. In both cases they often merge with female herds (Estes, 1991).

According to recent studies the giraffe herds represent a fission-fusion social system that is embedded in a larger community with changing size and composition of herds (Bercovitch et al., 2006; Bercovitch and Berry, 2010; Carter et al., 2013b). This system evolved in response to the exploitation of food availability that animals can most effectively use by broadcasting long-distance information to their kin. This is combined with short-distance bonding mechanisms (Bercovitch and Berry, 2012). Social ties in giraffe society could be influenced by kinship and social attraction or may only associate because they have similar habitat preferences (Carter et al., 2013a; Carter et al., 2013b).

Giraffes are known to use a *crèche* or nursery group care system in the wild (Langman, 1977; Leuthold, 1979; Pratt and Anderson, 1985). In captivity the social organization of herds also allows mothers to leave calves in the safe environment of a *crèche* group. They are tended by other giraffes, while they search for food (Greene et al., 2006). It is possible that these *crèche* groups may consist of related juveniles. Those bonds among juveniles and older females may persist through time (Bashaw et al., 2007).

Recent publication of Bashaw et al. (2007) demonstrated that captive giraffe females formed complex social structure with strong relationships. Further, experimental social separation of captive giraffes proved an importance of social relationships to a specific individual (Tarou et al., 2000). Other findings of Bashaw (2011) supported the fact that captive giraffe maintain strong relationships and suggested that studies of giraffe relationships were applicable across a range of captive conditions.

Giraffes have been widely distributed across African continent, forming a number of geographically distinctive forms classified at subspecies or species level (Groves and Grubb, 2011; Hassanin et al., 2007). Up to nine giraffe taxa have been recognized, differing in colour pattern and having probably strong environmental and behavioural mechanisms supporting their genetic segregation (Brown et al., 2007). Fission-fusion or similar association patterns have been described in Thornicroft's giraffe (*G. c. thornicrofti*) in Zambia (Bercovitch and Berry, 2010, 2012, 2013), West African giraffe (*G .c. peralta*) from Niger (Ciofolo et al., 2000; Le Pendu and Ciofolo, 1999; Le Pendu et al., 2000), Angolan giraffe (*G. c. angolensis*) in Namibia (Carter et al., 2013b; Fennessy, 2009), Reticulated giraffe (*G. c. reticulata*) in Kenya (Shorrocks and Croft, 2009; VanderWaal et al., 2014). Mother-calf relationships were studied in wild Cape giraffe (*G. c. giraffa*) in South Africa (Langman, 1977).

Contrastingly, studies of giraffe relationships in captivity focused on Rothschild giraffe (*G. c. rothschildi*) (Bashaw, 2011; Bashaw et al., 2007; Bercovitch et al., 2006), two focused on Reticulated giraffe (Greene et al., 2006; Perry, 2011), one focused on Massai giraffe (*G. c. tippelskirchi*) (Tarou et al., 2000).

Regarding giraffe taxa studied in the wild and in captivity, it is obvious that the comparison on the subspecies level can hardly be performed. However, very little is known about importance of social bonds when socially living animals face new environments (Fischer and Lindenmayer, 2000), either being transported to captive or to semi-captive conditions of fenced reserves. Recent efforts to enhance the effectiveness of translocation have focused on questions regarding the composition of founding populations, including social structure of translocated herds (Pérez et al., 2012). Moreover, study of social structure of giraffe in a new environment may help understanding of formation of social structure in giraffe and assess the possibilities of evolution of communal maternal care and formation of *crèche* groups in semi-captivity.

Aims and Hypotheses

Our aim was to assess the herd size and composition of Cape giraffes outside of their native range. (i) We predicted that giraffes were adapted to new environment and that group size and composition would be similar as in wild populations of other subspecies. We classify the dyads of giraffes according to strength of relationship (weak, medium and strong). (ii) We predicted that all dyads of female and filial juvenile would have strong relationships. (iii) Further, there would be some female dyads with strong relationship. We would then label those familiar females as "friends". (iv) From the findings connected with non-maternal care in giraffes we predicted that a female would develop a strong relationship with a calf of familiar female and that (v) the strength of the relationship between calves would depend on the strength of relationship between their mothers.

MATERIALS AND METHODS

Study area and destination

The social preferences of giraffes were observed in the Bandia reserve, Senegal, 15° 27' 0" North, 15° 24' 0" West (see Figure 1). The Bandia reserve is a fenced area (3 500 ha) created for safari-tourism and for the protection of the environment and wildlife. The Reserve is situated on the south-western border of the 'Classified Forest Bandia'. It is managed in public-private partnership since 1990 (Nežerková et al., 2004). The reserve belongs to the Sudan-Sahelian area (Antonínová et al., 2004). The ecosystem is flat with baobabs and dense shrubs. The original vegetation is composed by the variation of acacia species (Hejcmanová et al., 2010), with dominant *Acacia seyal* (Antonínová et al., 2004). This was the main nutrition source for giraffes in the

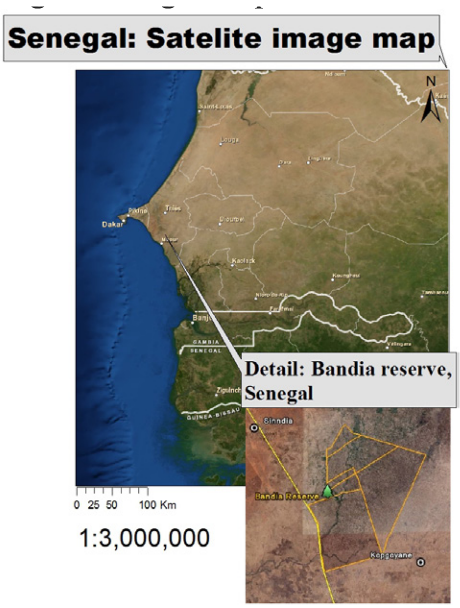

Figure 1. Senegal map with Bandia reserve location created in Gis10.2.

reserve. Two distinguished seasons characterize the climate: dry season (from November to June), and rainy season (from July to October) (White, 1983).

The representatives of native fauna in Bandia reserve include African warthogs (*Phacochoerus africanus*), patas monkeys (*Erythrocebus patas*) and green monkeys (*Chlorocebus sabaeus*). There are no native large predators in Bandia reserve, the largest carnivore is Golden jackal (*Canis aureus*).

Several mammalian species were imported into Bandia from Niokolo Koba National Park, e.g. African buffalo (*Syncerus caffer brachyceros),* Buffon's Kob (*Kobus kob),* West African roan *(Hippotragus equinus koba)*. In 2000, a group of Western Derby elands (*Taurotragus derbianus derbianus*) were introduced to the reserve and their conservation programme was started (Nežerková et al., 2004).

Further mammals were imported to Bandia reserve from South Africa to increase its attractiveness for tourism, e.g. Cape eland *(Taurotragus oryx oryx),* Great kudu *(Tragelaphus strepsiceros),* Impala (*Aepyceros melampus),* Gemsbok (*Oryx gazella gazella),* White rhino (*Ceratotherium simum simum)* and Cape giraffe.

The native giraffe subspecies in Senegal was West African giraffe, now surviving only in Niger (Brown et al., 2007; Ciofolo et al., 2009). This subspecies became extinct in Bandia before the announcement of the 'Classified Forest' in 1933 (Al Ogoumbrabe, 2002) and in 1954 disappeared form Niokolo Koba National Park (NKNP) and from the whole Senegal. In 1971 seven Kordofan giraffes (*G. c. antiqorum*) were translocated to NKNP in Senegal as they were assumed to be native subspecies (*G. c. peralta).* Recent research has proved this to be incorrect, because this subspecies was introduced into Niokolo Koba National Park from Cameroon (Al Ogoumbrabe, 2002) (see Figure 2). The translocation was unsuccessful, Kordofan giraffe did not adapt to new environment and all the giraffes died (Dupuy, 1972).

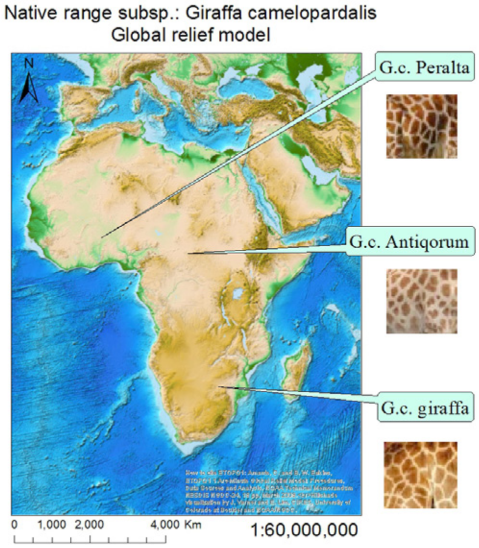

Figure 2. Native range and differences among giraffe subspecies historically found in Senegal.

In January 1997, four Cape giraffes were translocated from South Africa to the Bandia reserve (reserve managers, pers. comm). Giraffes adapted to new environment, reproduction started soon and there were already 10 individuals in Bandia in 2002 (Vincke et al., 2005). Two giraffes (sub-adult male and female) were relocated to Fathala reserve in Senegal in 2003 (Nezerkova-Hejcmanova et al., 2005) and further transfers were realized in 2006, 2008, and 2012 (reserve managers, pers. comm.). Except for the last years when our study has been performed, the relationships among individual giraffes remained unresolved.

Data collection

In total 28 giraffes (13 males, 15 females, see Table 1) were observed for 34 days in the dry season. Owing to Bandia reserve's requirements, all observations were recorded from a vehicle. Data was collected from the 27th January to the 9th March 2013. The identification of each

Table 1. List of observed giraffes in Bandia reserve, Senegal

Name	Number of observations	Sex	Age Category	Mother
Baobába	27	F	Adult	
Běla Uršula	34	F	Adult	
Bláža	28	F	Adult	
Dáša	29	F	Adult	
Hanča	30	F	Adult	
Liduška Beau Cou	28	F	Adult	
Terka	29	F	Adult	
Bětka	32	F	Subadult	
Dorotka	30	F	Subadult	
Maruška	30	F	Subadult	
Pavla	32	F	Subadult	
Lenka	30	F	Juvenile	Baobába
Majda	30	F	Juvenile	Běla Uršula
Markéta	29	F	Juvenile	Bláža
Růženka	30	F	Juvenile	Dáša
Lenin	26	M	Subadult	
Míša	27	M	Subadult	
Dušan	25	M	Juvenile	Liduška Beau Cou
Vilém	31	M	Juvenile	Terka
Bertík	31	M	Juvenile	Hanča
Unknown	12	M	Adult	
Józin	1	M	Adult	
Fall	9	M	Adult	
Bertrand	26	M	Adult	
Souhel	11	M	Adult	
Dan Jan	15	M	Adult	
Martin Absces	30	M	Adult	
Tom Michal	21	M	Adult	

individual was done in the first week. This was according to the unique coat drawing and significant signs which remain constant throughout life. Photographs of all giraffes within the study area were taken from both sides. Age classes were categorized as juvenile-male, juvenile-female, sub-adult male, sub-adult female, adult-male and adult-female. This was based on their size criteria and approximate age (Cameron and Dutoit, 2005). The genetic data were absent. We distinguished all mother-calf dyads according to the maternal behaviour, particularly suckling.

Data collection occurred generally during two sampling periods each day (8 to 11 am and 3 to 6 pm). The activity of the animals was the highest at this time. We were recording the group composition while driving on transects through the study area. At each sighting of a giraffe group, information was recorded about herd size, GPS position and identity of all individuals.

Association index (AI)

Many options have been proposed for calculating associations in animal societies (Cairns and Schwager, 1987; Ginsberg and Young, 1992; Wey et al., 2008; White and Smith, 2007; Whitehead et al., 2005). The most standard association indexes are affected by sample size. This is so that the dyad of individuals seen often will have a higher association index than those seen rarely (Whitehead, 2009; Whitehead et al., 2005). To describe giraffe social structure, we examined the dyadic associations between identified individuals. We refer to this measure as the ‘Association index’ (AI) where A and B refer to the identified individual. Based on Bercovitch and Berry (2012) we calculated the association index using following formula:

(A + B TOGETHER)/ [(A WITHOUT B) + (B WITHOUT A) + (A + B TOGETHER)] (Cairns and Schwager, 1987)

In the formula, (A + B TOGETHER) is the number of occasions A and B are seen together; (A WITHOUT B) is the number of occasions where A is seen without B. (B WITHOUT A) is the number of occasions B is seen without A. This index has the merit that all scores fall between 0, which means no association, and 1, which means complete association. Association, therefore, refers to the frequency when a dyad of individuals was observed in the same herd. Dyads consisted of any two individuals from the same group. If social preferences are consistently maintained over time, then they are considered relationships (Whitehead et al., 2005). We compared the levels of associations between giraffes in the Bandia reserve, with those reported for captive and wild giraffes residing in fission-fusion social systems (Bercovitch and Berry, 2012). According to the recorded AIs, we classified dyads into three categories: weak relationship (AI range 0 – 0.2), medium relationship (AI range 0.2 – 0.4), and strong relationship (AI range 0.4 – 1).

We further classified dyads into five types: male-male (includes any combination of AD, SUB, and JUV males except dyads of JUV males only), male-female (includes AD, SUB, and JUV males and females, except dyads of two JUV animals regardless the sex), female-female (includes any combination of AD, SUB, and JUV males except dyads of JUV females only and dyads of AD and filial JUV females), female-juvenile (includes AD female and a her filial JUV) , juvenile-juvenile (includes any dyad of JUV).

We labelled as “friends” the female-female dyads with strong relationships.

We recorded (i) size and composition of all sighted groups and we recorded all individuals, too. We classified the dyads of giraffes according to strength of relationship (weak, medium and strong) and we compared the mean AIs for all types of dyads using Kruskal-Wallis test (the data distribution was not normal). (ii) We assessed the AIs of all dyads of females and their filial juveniles. (iii) We further assessed the AIs of female-female dyads to find out whether strong relationships would occur in some of them. We would then label those familiar females as “friends”. (iv) We compared the AIs among females and juveniles (filial calf, calf of a friend, calf of non-friend) using Kruskal-Wallis test. Last, using Spearman correlation, we tested (v) the relation of strength of the relationship between calves and the strength of relationship between their mothers.

RESULTS

In total, 144 giraffe contacts (88 groups of two or more individuals and 56 individual sightings) were recorded in 34 days. (i) The average number of individuals in the group was 7.22 ± 4.06 (range 2-17).

Any two animals were seen together 7 ± 0.35 times (range 0-26). We reported weak relationships ($AI < 0.2$, $n = 251$) and medium relationships ($0.2 < AI < 0.4$, $n = 91$) in all types of dyads except female-juvenile. We reported strong relationships ($AI > 0.4$, $n = 32$) in two types of dyads (female-female and female-juvenile). From 378 possible dyads giraffes were observed in 313 dyads. The hypothetic dyads, which were never observed, always included an adult male either with another male or female. From 56 encounters with solitary individuals there was only one female.

Observed dyads (excluding dyads never observed together) revealed mean AI of 0.19 ± 0.16 (range 0.02 – 0.76, n = 313). We reported weak relationships (n = 251) and medium relationships (n = 91) in all types of dyads except female-juvenile. We reported strong relationships (n = 32) in two types of dyads (female-female and female-juvenile). The AIs significantly differed among types of dyads ($H_{(4, n=313)} = 86.012$, $p < 0.0001$, Figure 3).

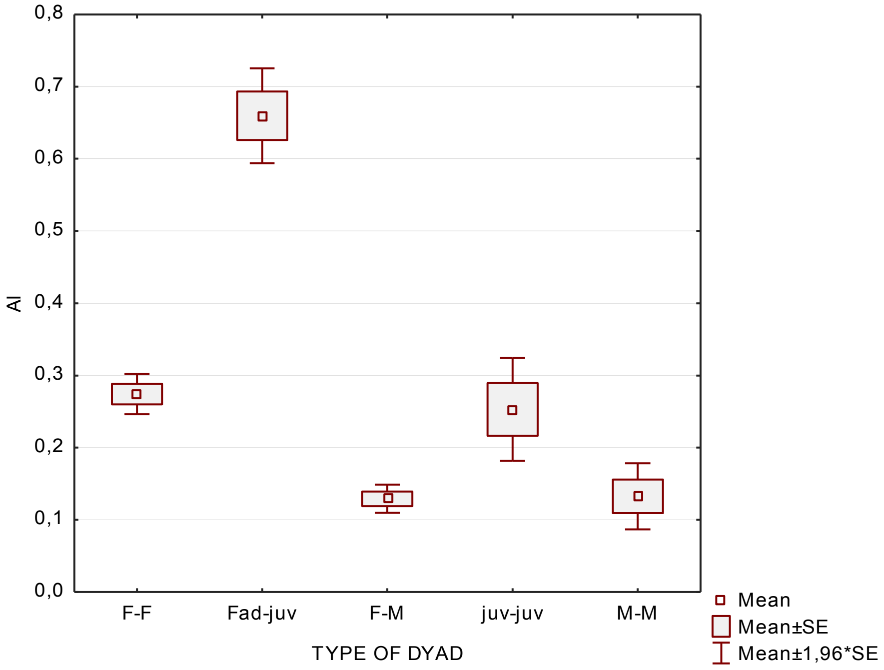

Figure 3. Mean AI for five dyad types showing the highest value for mother-offspring dyads. N values for specified types of dyads are following: female-female F-F N = 95, female and filial offspring Fad-juv N = 7, female-male F-M N = 184, juvenile-juvenile juv-juv N = 15, M-M N =77

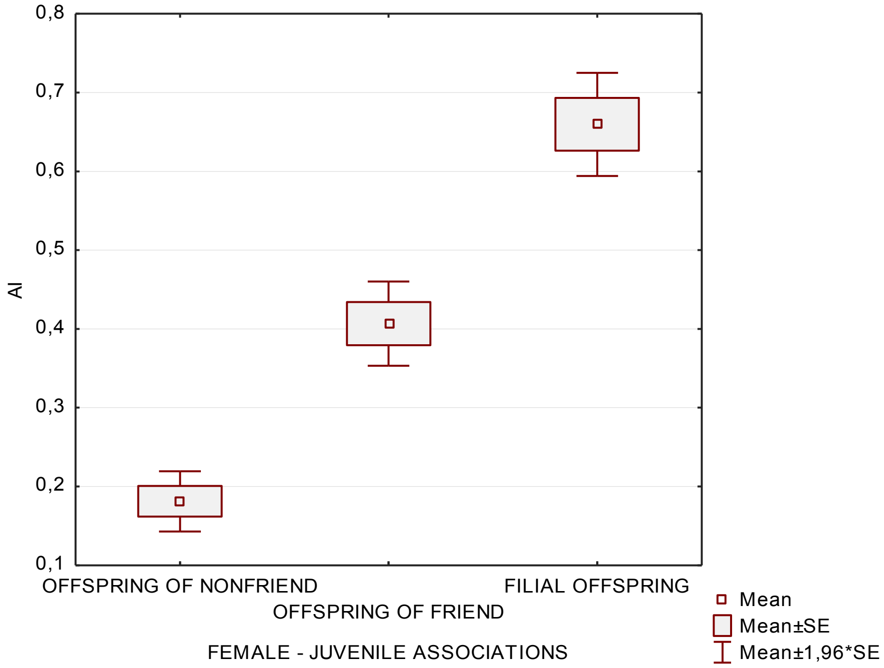

Figure 4. Differences in AI in female-juvenile associations showing the difference between AI with filial calf, calf of a friend and calf of a non-friend. N values for specific association types are: offspring of non-friend N = 36, offspring of friend N = 6, filial offspring N = 7

Mean AI (ii) between females and their filial calves was 0.66 ± 0.09 (range 0.50 – 0.76, n = 7), the highest of all dyad types. All female-juvenile pairs demonstrated strong relationship.

The mean AI among adult females was 0.22 ± 0.15 (range 0.03 – 0.54, n = 21). We found strong relationship (iii) in three dyads of female giraffes (Baobába – Hanča AI = 0.46, Běla Uršula – Dáša AI = 0.54, Liduška Beau Cou – Terka

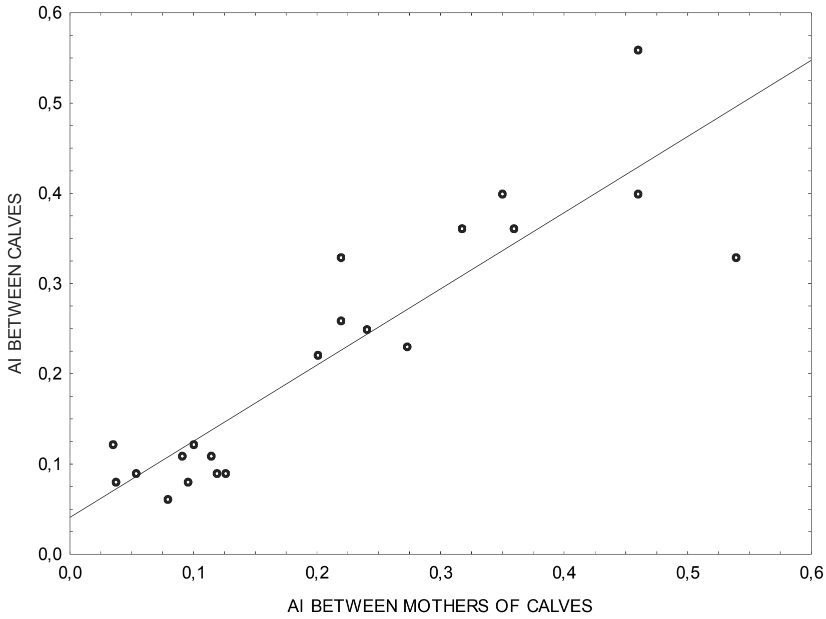

Figure 5. The higher the AI between mothers, the higher the AI between their calves.

AI = 0.46). We labelled those female dyads as "friends". Each of adult females had just one friend, only female Bláža remained strongly associated only to her filial calf.

(iv) Adult female giraffes were associated more often with the calves of familiar females than with the calves of other adult females ($H_{(2, n=49)} = 26.25$, $p < 0.001$; Figure 4). Relationships between females and calves of their friends were medium to strong (mean AI = 0.41 ± 0.07, range 0.31 – 0.46, n = 6). Relationships between females and calves of non-friends were weak to medium (mean AI = 0.18 ± 0.12, range 0.05 – 0.38, n = 36).

(v) The higher was the AI between females, the higher was the AI of their calves (Spearman coef. = 0.86, $p < 0.001$; Figure 5).

DISCUSSION

During our study we recorded 88 groups of two or more individually recognised giraffes. (i) The average number of individuals in a group was more than seven. This was slightly higher than in most of the studies from the wild, where usually five to six giraffes formed a group (Le Pendu et al., 2000; Leuthold and Leuthold, 1978; Shorrocks and Croft, 2009; van der Jeugd and Prins, 2000; VanderWaal et al., 2014). The number of individuals seen together in a group varied from two to 17. Group size in Bandia reserve could have been affected by limited space in fenced area, resulting in slightly larger group size. Nevertheless, giraffe density, home-range size, and group stability was found to differ across different habitats (van der Jeugd and Prins, 2000). The group size of observed giraffes in the Bandia reserve was comparable to those in the native range of other subspecies.

All but one sightings of solitary individuals were males. This corresponds to general grouping patterns of giraffes in other studies. Males may be found in groups or solitary, but females are mainly aggregated, even in a different habitat (Bercovitch and Berry, 2012, 2013; Carter et al., 2013a; Le Pendu et al., 2000). Sexual segregation of males is not connected only with sociality but may be connected with food selectivity (Estes, 1991). Younger males actively prefer to associate with animals of similar age, whereas older males, which tend to dominate mating opportunities, avoid associating with rivals (Pratt and Anderson, 1982).

The average AI in our study (excluding dyads which were never observed together) was 0.19 (range 0.02-0.76). This value is slightly higher than 0.12 as published by Bercovitch and Berry (2012) for wild giraffes. The higher AI corresponds to with greater group size reported in fenced Bandia reserve. Most of the dyads (male-male, male-female and part of the female-female dyads) did not regularly associate together, as reported by other studies (Bercovitch and Berry, 2013; Carter et al., 2013a).

(ii) The highest values of AI in mother-calf dyads corresponds to with findings from both captive and wild populations (Bashaw et al., 2007; Bercovitch and Berry, 2012). Giraffe cow reactions to their dead calves provide evidence that a mother-calf bond develops from birth (Bercovitch and Berry, 2012; Strauss and Muller, 2013) and may persist for years (Carter et al., 2013b). Such a long-term relationship would have an important influence on further association patterns of adult giraffes, resulting in formation of female-bonded kin groups.

We reported the mean AI among adult females as 0.22 ± 0.15, similar to other studies using the same AI formulae (Bercovitch and Berry, 2012; Perry, 2011). Cape giraffes in Bandia showed higher associations among females than wild Thornicroft's giraffe in Luangwa, Zambia, 0.17 ± 0.15 (White and Smith, 2007; Bercovitch and Berry, 2013). Moreover, we found strong relationship (AI > 0.4) in three of 21 possible giraffe female dyads, corresponding to results of Bashaw et al. (2007). Surprisingly, each of the females had just one preferred "friend", resulting in formation of three dyads of "friends" and one remaining female with strong relationship to her filial calf only. The familiar females made only dyads; no trio with strong relationship was reported. Nevertheless, the number of females in our study was very low and the level of "strong relationship" was set up arbitrary. The formation of relationships among adult female giraffe should be further tested.

Regardless the limits of the method used for associations measures, the female dyads shown non-random preference to spend time with specific individual in the same group. Patterns of giraffes associations are variable. It is possible that long-lived females experience social preferences and avoidances based on previous experiences over many years with known conspecifics (Carter et al., 2013b). It is also possible that mother–daughter or sister relationships could persist through the time (Bashaw et al., 2007). Potential advantages gained by females from associating strongly with a particular female include increased reproductive output, increased survival and psychological wellbeing (Leuthold, 1979). Stronger bonds among females may have adaptive function due to reciprocity and allomaternal care. As we do not know genetic relationships among adult and subadult individuals, we cannot assess whether the strong association persists there for years as in wild populations.

(iv) In our study adult female associated more often with a calf of familiar female (friend) than with a calf of other females. Relationships between females and calves of their friends were medium to strong and relationships between females and calves of non-friends were weak to medium. Calves of these familiar females associated together and formed a *crèche* more often than the calves of non-familiar females. This corresponds with result of Pratt and Anderson (1985) on wild giraffes. The *crèche* cohesion seems to be tighter when strong social bonds exist among mothers and giraffe's calves reared in a *crèche* have a higher probability of survival than those reared alone (Bercovitch and Berry, 2012). It is possible that personal preferences for particular conspecifics are formed in giraffe *crèche* groups (Leuthold, 1979).

Female giraffe social structure in captivity appears to reflect a continuation of mother-calf attachment (Bejder and Fletcher, 1998) and promoted allomaternal care, including allonursing. Calves' preferences for females could emerge from allomothering activities according to Perry (2011). In the wild allomothering was reported rarely, but at least one successful allonursing event was documented (Pratt and Anderson, 1985). Nevertheless, relatedness and stable composition of the herd in captivity could increase these allomothering activities.

(v) The strength of the relationship between calves depended on the strength of relationship between their mothers. This corresponds with results of Bercovitch and Berry (2013) that giraffe calves born into the same cohort have stronger social associations than calves born into different age cohorts. Association patterns of females may influence further associations in their calves, as the relationships among cohort members may persist for a long time.

CONCLUSIONS

Our research has shown that even with a small number of founders the translocation of Cape giraffes to new environment was successful. Females showed normal reproducing pattern and their social system was similar to native range and as in other giraffe subspecies across different environment. We confirmed that giraffes show non-random social preferences and that the relationships among females influence the relationships among their calves.

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6. DISCUSSION AND CONCLUSION

All the articles included in this thesis are new results from the social life of giraffes. Based on my results, it is clear that giraffes, formerly considered to be animals with weak social bonds (Estes 1991), might form a hierarchy (at least in the zoo environment), make friends (both in captivity as well as in the wild) and very frequently allonurse young who were probably the calves of females to which they have a closer social bond.

I have tested seven hypotheses explaining allonursing based on the rejection rate. These results provide evidence for reciprocal help as a potential explanation of giraffe females allonursing. Further, I would like to also analyse the frequency and duration of allonursing. Although many studies have concluded that the correlation between the frequency and duration of suckling and total milk transfer was very weak or non-existent (Mendl & Paul 1989; Birgersson & Ekvall 1994; Cameron 1999b), these parameters represent a good indicator of parent-offspring conflict (Mendl & Paul 1989; Therrien et al. 2007). Therefore, it would be interesting if the analyses of allonursing bout duration and frequency would support the same hypotheses as the rejection rate.

The allosuckling behaviour of calves was in line with the hypothesis of milk theft. They exploit the opportunity of filial nursing and join in mostly from behind. In these positions it is difficult for the female to identify the calves. Two additional hypotheses might explain why the calves need to steal the milk – the compensation hypothesis and improved nutrition hypothesis. Both of them are connected with the growth and weight of animals. However, very few previous studies focused on the basic information about giraffe weight and growth. These studies are old, and do not indicate the sample size or the subspecies of giraffe (Dorst et al. 1972; Wilson 1969; Hall-Martin 1976; Hall-Martin 1977). Therefore, I started by determining the growth functions of male and female giraffes and calculated the weight gains during giraffe ontogeny, which resulted in the article entitled “The Weight of Rothschild Giraffe—Is It Really Well Known?” as the Prague Zoo used to weigh giraffes regularly and I obtained this unique data set to analyse. Thus, in the future I would like to combine this data with allosuckling data to verify the above hypotheses.

To test the hypothesis of social benefits, which assumes that females preferentially allonurse the offspring of dominant females (Baldovino & Di Bitetti; 2008; Roulin 2002), the hierarchy had to be tested, which can be found in the article “The First Description of Dominance Hierarchy in Captive Giraffe: Not loose and Egalitarian, but Clear and Linear“. The article is the first study to describe the hierarchy in captive giraffes. In general, the hierarchy could not be determined only on the basis of agonistic interaction, but on avoidance (Elliot 2006). In our study, we included avoidance as well as other agonistic interactions. In some mammals like equids, studies have shown that the measuring of avoidance and of aggressive interactions resulted in the same hierarchy (Pluháček et al. 2006; Côté 2000). In our study almost the half of all the observed interactions could be assigned to avoidance, as giraffes are primarily not aggressive (Le Pendu 2000). The second most numerous interaction was pushing. Necking was recorded mostly in males, which corresponds with the results from the wild (Coe 1967; Simmons & Scheepers 1996). In the wild, no hierarchy among giraffe females has been recorded. Nevertheless, in the Bandia reserve in Senegal I observed several cases of avoidance among adult giraffe females (unpublished data). This could indicate a clear preadaptation for hierarchy formation. Thus, it should be further worth investigating if any degree of hierarchy also exists in giraffes in the wild.

The manuscript “Giraffe nursing behaviour reflects environmental conditions” is one of the few studies which deals with the proximate factors of nursing (Jensen 1988; Hejcmanová et al. 2011). Furthermore, the research was done by the same observer using the same method in both environments, which is really a unique situation. Although more data would be better, this study provides unique results, as only a few other studies focused on the social behaviour of ungulates compares the two environments (Hejcmanová et al. 2011). This manuscript found a higher occurrence of allonursing in the zoo than in the reserve, which corresponds with the previous assumption (Packer 1992). In giraffes, only one case of allonursing in the wild has been published to date. However, many researchers confirmed that they have seen adult giraffes nursing more than one calf, taking into account that only one was filial and thus the other had to be non-filial. On the other hand, in the Bandia reserve in Senegal I observed no successful allonursing, although several attempts of calves to suckle from a non-maternal female were noticed. I would like to stress that these calves preferred to attempt to suckle from the females which were friends of their mother (unpublished results). This could result from the fact that females associated more frequently with the calves of their friends than with the calves of non-friend females. Nevertheless, these results show that allonursing could occur in any environment. The higher incidence of allonursing in captivity could be associated with the higher population density. Thus, for giraffes, the captive conditions might amplify the strong pre-adaptation to allonurse to an extent which is one of the highest among mammals.

This thesis compiles new results from various aspects of social behaviour which were found due to the study of communal parental care, allonursing. I think that these results are not only important for our knowledge of giraffes, but I believe that they could be useful for studying mammalian behaviour in general. In addition, these results came from a “well known animal” species which has not been explored as much as it deserves. Currently, the reproduction of giraffes in European zoos is limited due to management purposes and due to psychological reasons within the European human population. Therefore, in these days such a data set cannot be collected as easily as it was in the past, which I think makes my results even more important. Last but not least, the conclusions from both environments have an applicable use for the keepers and managers of the reserve and zoos, especially in connection with the weight and health condition of the animals in the zoo and to clarify the number of animals and their habitat preferences in the nature reserve.

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Appendix 2: Herd composition and changes in individual zoos

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Table 2: Herd composition inf Olomouc zoo

Table 3: Herd composition in Liberec zoo

Table 4: Herd composition of Rothschild's giraffes in Dvůr Králové zoo

Table 5: Herd composition of Reticulated giraffes in Dvůr Králové zoo

Appendix 3: Feed ration in individual zoos

Table 1: Feed ration in Prague zoo

Table 2: Feed ration in Olomouc zoo

Table 3: Feed ration in Liberec zoo

Table 4: Feed ration in Dvůr Králové zoo

Appendix 1: Overview of allonursing for individual species

Species	Common name	Taxon	Possible explanation of allonursing	Source
Acomys dimidiatus	Sinai spiny mice	Rodentia	Misdirected parental care	Tučková et al. 2016
Alcelaphus buselaphus	Coke‘s hartebeest	Cetartiodactyla	Missing	R.D. Estes - pers. com. In Packer et al. 1992
Alouatta palliata	Mantled howler	Primates	Adoption	Clarke & Glander 1981
Ammotragus	Barbary sheep	Cetartiodactyla	Missing	Cassinello 1999
Antilocapra americana	Pronghorn	Cetartiodactyla	Milk theft	J. Byers - pers. com. In Packer 1992
Apodemus sylvaticus	Wood mouse	Rodentia	Kin selection	Gerlach & Bartmann 2002
Arctocephalus forsteri	New Zealand fur seal	Carnivora	Milk theft	Dowell 2005
Arctocephalus tropicalis	Subantarctic fur seal	Carnivora	Milk theft	dey Bruyn 2009
Artocephalus galapagoensis	Galapagos fur seal	Carnivora	Milk theft	Trillmich 1981
Axis axis	Chital	Cetartiodactyla	Missing	Schaller 1967
Bison bison	Bison	Cetartiodactyla	Reciprocity*	J. Berger & J. Wolff - pers. com. In Packer et al. 1992; Jones & Treanor 2008
Bos primigenius	Cattle	Cetartiodactyla	Compensation	Víchová & Bartoš 2005
Bos taurus	Cattle	Cetartiodactyla	Milk theft	Lidfords & Jensen 1988
Bubalus bubalis	Water buffalo	Cetartiodactyla	Misdirected parental care	Murphey et al. 1991; 1995
Callinthrix flaviceps	Buffy-headed marmoset	Primates	Missing	Guimaraes 1998
Callinthrix jacchus	Common marmoset	Primates	Social benefit	Digby 1995
Camelus bactrianus	Camels	Cetartiodactyla	Milk theft	Brandlová et al. 2013
Canis familiaris	Free-ranging dogs	Carnivora	Kin selection and milk theft	Paul & Bhadra 2016
Canis lupus	Wolf	Carnivora	Missing	Packard et al. 1985
Canis patrans	Coyote	Carnivora	Missing	Camenzind 1978
Capra hircus	Feral goat	Cetartiodactyla	Missing	R. Dunbar & P. Klopfer - pers. com. In Packer et al. 1992
Carollia perspicillata	Short-tailed fruitbat	Chiroptera	Missing	T. Fleming - pers. com. In Packer et al. 1992
Cavia aperea	Cavy	Rodentia	Missing	Rood 1972

Species	Common name	Taxon	Possible explanation of allonursing	Source
Cavia porcellus	Domestic guinea pig	Rodentia	Improved nutrition and milk theft	Fullerton et al. 1974; Takamatsu 2007
Cebus capucinus	White-faced capucin	Primates	Reciprocity	Manson, 1999; Sargeant et al. 2015
Cebus nigritus	Tufted capuchin monkeys	Primates	Social benefit	Baldovino & Bitetti 2007
Cebus olivaceus	Wedge-capped capuchin	Primates	Social benefit	T.G. O Brien - pers. com. In Packer et al. 1992
Cervus elaphus	Red deer	Cetartiodactyla	Milk theft, improved nutrition and misdirected parental care	F. Guiness & M. Marquez - pers. com. In Packer et al. 1992; Bartoš et al. 2001ab; Drábková et al. 2008
Cervus elaphus hispanicus	Iberian red deer	Cetartiodactyla	Compensation	Landete-Castillejos et al. 2000
Connchaetes taurinus	Wildebeeste	Cetartiodactyla	Missing	Estes & Estes 1979
Crocuta crocuta	Spotted hyaena	Carnivora	Kin selection and social benefit	M. East, L. Frank, H. Hofer, K. Holekamp, G. Mills & L. Smale - pers. com. In Packer et al. 1992; Knight et al. 1992
Cynomys ludovicianus	Black-tailed prairie dog	Carnivora	Kin selection	Hoogland et al. 1989
Cynomys parvidens	Utah prairie dogs	Carnivora	Reciprocity and kin selection	Hoogland 2009
Dama dama	Fallow deer	Cetartiodactyla	Kin selection and compensation	Ekvall, 1998; Pélabon et al. 1998
Delphinapterus leucas	Beluga	Cetartiodactyla	Missing	Leung et al. 2010
Ectophylla alba	Honduran white bat	Chiroptera	Milk theft	A. Brooke - pers. com. In Packer et al. 1992
Elephas maximus	Asiatic elephant	Proboscidea	Missing	McKay 1973; Vidya 2014
Enhydra lutris nereis	California sea otter	Carnivora	Milk theft	M. Riedman - pers. com. In Packer et al. 1992
Equus burchellii	Plains zebra	Perissodactyla	Adoption	Jan Pluháček et al. 2011
Equus caballus	Horse	Perissodactyla	Milk theft	S. Crowell - Davis; R. Keiper - pers. com. In Packer et al. 1992
Equus caballus	Feral horse	Perissodactyla	Kin selection	Nunez et al. 2013; Cameron et al. 1999a
Equus grevyi	Grevy‘s zebra	Perissodactyla	Reciprocity?	Olleova et al. 2012
Erythrocebus patas	Patas monkey	Primates	Missing	J. Chism & T.E. Rowell - pers. com. In Packer et al. 1992
Eumatopia jubatus	Steller sea lion	Carnivora	Milk theft	L. V. Higgins - pers. com. In Packer et al. 1992; Maniscalco et al. 2007
Felis catus	Domestic cat	Carnivora	Missing	Macdonald et al. 1987
Galea musteloides	Cuis	Rodentia	Milk theft	Rood 1972

Species	Common name	Taxon	Possible explanation of allonursing	Source
Giraffa camelopardalis	Giraffe	Cetartiodactyla	Milk theft	Pratt & Anderson 1979
Halichoeris grypus	Grey seal	Carnivora	Missing	Kovacs 1987
Helogale parvula	Dwarf mongoose	Carnivora	Kin selection and social benefit	N. & S. Creel & J. Rood - pers. com. In Packer et al. 1992; Creel et al. 1991
Heterocephalus glaber	Naked mole-rat	Rodentia	Missing	Ciszek 2000
Heterohyrax brucei	Bush hyrax	Hyracoidea	Milk theft	Hoeck 1982
Hippopotamus amphibius	Common hippopotamus	Cetartiodactyla	Kin selection *	Pluháček & Bartošová 2011
Hyaena brunnea	Brown hyaena	Carnivora	Kin selection and social benefit	G. Mills; D. & M. Owens; M. Knight & A. van Jaarsveld - pers. com. In Packer et al. 1992
Hydrochoreus hydrochoreus	Capybara	Rodentia	Missing	Macdonald 1981
Chlorocebus aethiops	Green monkey	Primates	Milk theft	L. Fairbanks - pers. com. In Packer et al. 1992
Lama guanicoe	Guanacos	Cetartiodactyla	Milk theft and compensation	Zapata et al. 2009ab; 2010
Lemur catta	Ringtail lemur	Primates	Kin selection and parenting	Pereira & Izard 1989; Gould 1992
Leptonychotes weddelli	Weddell seal	Carnivora	Milk theft	Kaufman et al. 1975
Loxodonta africana	African elephant	Proboscidea	Kin selection	P.C. Lee - pers. com. In Packer et a. 1992
Lycaon pictus	African wild dog	Carnivora	Kin selection	J. Malcolm per com In Packer et a. 1992
Macaca fuscata	Japanese macaque	Primates	Kin selection	Tanaka 2004
Macaca mulatta	Rhesus macaque	Primates	Kin selection	Berman 1982
Macaca radiata	Bonnet macaque	Primates	Missing	J. Silk - pers. com. In Packer etal. 1992
Macropus agilis	Agile wallaby	Diprotodontia	Missing	Merchant 1976
Macropus giganteus	Eastern grey kangaroo	Diprotodontia	Misdirected parental care	King et al. 2015
Meles meles	European badger	Carnivora	Missing	Dugdale et al. 2010
Microcavia australis	Dwarf cavy	Rodentia	Missing	Rood 1972
Microcebus murinus	Gray mouse lemur	Primates	Kin selection	Eberle & Kappeler 2006
Miopithecus talapoin	Talapoin monkey	Primates	Missing	Chism 1980
Mirounga angustirostris	Northern elephant seal	Carnivora	Milk theft	Le Boeuf et al. 1972; Riedman & Le Boeuf 1982

Species	Common name	Taxon	Possible explanation of allonursing	Source
Monachus schauinslandi	Hawaiian monk seal	Carnivora	Misdirected parental care	Boness 1990
Mungos mungo	Banded mongoose	Carnivora	Missing	J. Rood - pers. com. In Packer et al. 1992
Mus musculus	House mouse	Rodentia	Reciprocity and kin selection	J. Manning & W. Potts - pers. com. In Packer et al. 1992; Konig 2006
Nasua narica	Coati	Carnivora	Missing	Russell 1983
Neophoca cinerrea	Australian sea lion	Carnivora	Missing	L. V. Higgins - pers. com. In Packer et al. 1992; Pitcher at al. 2011
Nycticeius humeralis	Evening bat	Chiroptera	Milk evacuation	G. Wilkinson - pers. com. In Packer et al. 1992; Wilkinson 1992
Octodon degus	Degu	Rodentia	Kin selection	Ebensperger et al. 2002
Ochotona curzoniae	Black-lipped pika	Lagomorpha	Milk theft	A. Smith - pers. com. In Packer et al. 1992
Otocyon megalotis	Bat-eared fox	Carnivora	Kin selection	B. Maas - pers. com.in Packer et al. 1992; Pauw 2000
Ovis gmelini musimon	Mouflon	Cetartiodactyla	Compensation?	Réale et al. 1999
Panthera leo	African lions	Carnivora	Kin selection	A.E. Pusey & C. Packer - pers. obs. In Packer et al. 1992; Pusey & Packer 1994
Papio cynocephalus	Yellow baboon	Primates	Milk theft and social benefit	J. Altman & S. Wasse - pers. com. In Packer et al. 1992
Peromyscuss maniculatus	Deer mouse	Rodentia	Missing	Packer et al. 1992
Phacochoerus aethiopicus	Warthog	Cetartiodactyla	Kin selection	Bradley 1968; Plesner Jensen et al. 2000
Phyllostomus hastatus	Greater spear-nosed bat	Chiroptera	Missing	J. Bradbury - pers. com. In Packer et . 1992
Physeter macrocephalus	Sperm whales	Cetartiodactyla	Reciprocity and kin selection	Gero et al. 2009
Pipistrellus pipistrellus	Pipistrelle bat	Chiroptera	Misdirected parental care	Kleiman 1969; Fanis & Jones 1996
Presbytis entellus	Hanuman langur	Primates	Milk theft	S.B. Hrdy - pers. com. In Packer et a. 1992
Procavia johnsotni	Rock hyrax	Hyracoidea	Milk theft	Hoeck 1982
Propithecus candidus	Silky Sifaka	Primates	Missing	Thalmann et al. 2007

Species	Common name	Taxon	Possible explanation of allonursing	Source
Rangifer tarandus	Reindeer	Cetartiodactyla	Milk theft, kin selection, reciprocity	Epsmark 1971; Engelhardt et al., 2014; 2015; 2016ab
Saguinus mystax	Moustached tamarin	Primates	Missing	Smith et al. 2001
Saimiri boliviensis boliviensis	Bolivian Squirrel Monkey	primates	Missing	Milligan et al. 2008
Senegalensis braccatus	Senegal galago	Primates	Missing	Kessler & Nash 2010
Suricata suricatta	Meerkat	Carnivora	Social benefit	S.P. Doolan & D.W. Macdonald - pers. com. In Packer et al. 1992; Doolan & Macdonald 1999; MacLeod et al. 2013
Sus scrofa	Pig	Cetartiodactyla	Milk theft	Packer et al. 1992; Illmann et al. 2007
Syncerus caffer	Cape buffalo	Cetartiodactyla	Missing	F. Mizutani - pers. com. In Packer et al. 1992
Tadarida brasiliensis	Mexican free-tailed bat	Chiroptera	Misdirected parental care	McCracken - pers. com. In Packer et al. 1992
Tayassu tajacu	Collared peccary	Cetartiodactyla	Kin selection	Byers & Bekoff 1981; Byers 1983; Babbit & Packard 1990
Trichechus manatus	Florida manatee	Sirenia	Milk theft	T.J. O Shea - pers. com. in Packer et al. 1992
Tursiops aduncus	Bottlenose dolphin	Cetartiodactyla	Missing	Sakai et al. 2016
Ursus maritimus	Polar bear	Carnivora	Misdirected parental care	Lunn et al. 2000
Varecia variegata	Ruffed lemur	Primates	Kin selection	Pereira et al. 1987
Vulpes vulpes	Red fox	Carnivora	Kin selection and social benefit	Macdonald 1979
Zalophus californianus	California sea lion	Carnivora	Milk theft	Ono et al. 1987

***** Extremely limited sample size

? Merely a plausible explanation (not directly tested, arises from the text)

Appendix 2: Herd composition and changes in individual zoos

Table 1: Herd composition in Prague zoo

Name	Sex	Age category	Birth Date	Place of birth	Date of loss
			Date of increment	**Where from**	**How / Where**
Šimon	M	Adult	21.12.1986	Praha	6.5.2009
Berta	F	Adult	25.3.1988	Köln	
Kleopatra	F	Adult	13.1.1993	Dvůr Králové	
			13.4.1994	Transport to Praha	
Eliška	F	Adult	6.10.1995	Praha	
Nikola	F	Adult	28.11.1997	Praha	30.3.2010
Nora	F	Adult	27.6.1999	Praha	
Diana	F	Adult	6.1.2003	Praha	
Johan	M	Adult	20.12.1999	Rhenen	
Kasunga	F	Adult	2.7.2000	Olomouc	30.7.2009
Marek	M	Young	25.4.2006	Praha	5.5.2008
Hana	F	Young	16.8.2006	Praha	1.7.2009
Dagmar	F	Young	20.12.2006	Praha	7.3.2008
Inka	F	Young	26.1.2007	Praha	21.4.2008
Sandra	F	Young	23.8.2007	Praha	14.10.2008
Luděk	M	Young	26.8.2007	Praha	15.4.2009
Václav	M	Young	28.9.2007	Praha	15.4.2009
Mahulena	F	Young	17.11.2007	Praha	23.6.2009
Bořek	M	Young	11.7.2008	Praha	13.5.2010
Slávek	M	Young	19.1.2009	Praha	15.12.2010
Bedřiška	F	Young	1.3.2009	Praha	21.3.2011
Gabriela	F	Young	8.3.2009	Praha	
Jiří	M	Young	28.4.2009	Praha	10.11.2010
Laura	F	Young	30.5.2009	Praha	21.3.2011
Farra	F	Young	30.10.2007	Rapperswill	
			24.6.2009	Transport to Praha	
Jakub	M	Young	24.7.2010	Praha	

Name	Sex	Age category	Birth Date	Place of birth	Date of loss
			Date of increment	Where from	How / Where
František	M	Young	14.10.2011	Praha	
Vilma	F	Young	6.1.2011	Praha	
Doubravka	F	Young	23.1.2011	Praha	

Table 2: Herd composition in Olomouc zoo

Name	Sex	Age category	Birth Date	Place of birth	Date of loss
			Date of increment	Where from	How / Where
Veronika	F	Adult	15.12.1988	Olomouc	
Amina	F	Adult	23.10.1994	Olomouc	
Kimberley	F	Adult	20.3.1998	Dvůr Králové	
			15.4.1999	Transport to Olomouc	
Zaira	F	Adult	14.5.2000	Olomouc	
Lerbie	F	Adult	7.11.2002	Olomouc	
Samantha	F	Adult	31.5.2004	Olomouc	
Marc	M	Adult	24.5.2003	Arnhem	
			24.5.2006	Transport to Olomouc	
Susanne	F	Young	2.5.2008	Olomouc	
Natasa	F	Young	19.5.2008	Olomouc	
Pavlina	F	Young	6.4.2009	Olomouc	
Kayla	F	Young	17.1.2010	Olomouc	
Zainabu	F	Young	26.2.2010	Olomouc	
Wambua	M	Young	12.5.2010	Olomouc	

Table 3: Herd composition in Liberec zoo

Name	Sex	Age category	Birth Date	Place of birth	Date of loss
			Date of increment	**Where from**	**How / Where**
Nancy	F	Adult	30.3.1993	Liberec	
Sandra	F	Adult	27.1.2000	Liberec	21.4.2008
Sulika	F	Adult	29.3.1985	Dvůr Králové	5.4.2009
			16.4.1986	Transport to Liberec	
Kimi	M	Young	24.7.2007	Liberec	20.4.2009
Mike	M	Young	24.8.2006	Arnhem	
Nela	F	Young	21.4.2008	Liberec	
Nisa	F	Young	24.5.2008	Liberec	
Sangha	F	Young	7.3.2006	Liberec	16.11.2008
Twiga	F	Young	9.12.2006	Liberec	

Table 4: Herd composition of Rothschild's giraffes in Dvůr Králové zoo

Name	Sex	Age category	Birth Date	Place of birth	Date of loss
			Date of increment	**Where from**	**How / Where**
Viola	F	Adult	3.4.1982	Dvůr Králové	19.11.2010
Ali	M	Young	22.6.2009	Dvůr Králové	10.8.2010
Jan	M	Young	25.7.2009	Dvůr Králové	10.8.2010
Noel	M	Young	26.7.2008	Dvůr Králové	16.9.2010
Vilem	M	Young	15.12.2007	Dvůr Králové	11.8.2009
Kimi	F	Adult	6.2.1990	Dvůr Králové	
Mick	M	Young	2.8.2011	Dvůr Králové	
Jenifer	F	Young	11.2.2007	Dvůr Králové	
Raha	F	Young	10.11.2011	Dvůr Králové	
Jaruna	F	Adult	2.7.1997	Olomouc	
Johan	M	Young	23.8.2011	Dvůr Králové	
Kenia	F	Adult	2.5.2000	Barcelona	
Akin	M	Young	7.10.2001	Dvůr Králové	

Name	Sex	Age category	Birth Date	Place of birth	Date of loss
			Date of increment	Where from	How / Where
Viktoria	F	Adult	1.11.2001	Dvůr Králové	
Tery	M	Young	18.8.2010	Dvůr Králové	
Etola	F	Adult	20.11.2001	Dvůr Králové	
Edgar	M	Young	12.8.2011	Dvůr Králové	
Ozák	M	Young	5.1.2010	Dvůr Králové	
Ella	F	Adult	26.9.2005	Dvůr Králové	
Legas	F	Young	7.7.2010	Dvůr Králové	
Johari	F	Adult	5.10.2006	Hannover	
			28.5.2008	transport to DK	
Nina	F	Adult	12.7.1997	Liberec	
			10.7.1998	transport to DK	
Tommy	M	Adult	2.3.2002	Rhenen	
			13.5.2004	transport to DK	

Table 5: Herd composition of Reticulated giraffes in Dvůr Králové zoo

Name	Sex	Age category	Birth Date	Place of birth	Date of loss
			Date of increment	Where from	How / Where
Julie D	F	Adult	23.5.2003	Dvůr Králové	
Justina	F	Young	27.8.2011	Dvůr Králové	
Julie B	F	Adult	8.12.2006	Brno	
			11.4.2008	Transport to DK	
Joachim	M	Young	12.10.2011	Dvůr Králové	
Brindisi	F	Adult	28.12.1989	Dvůr Králové	
Bazyl	M	Young	1.11.2011	Dvůr Králové	
Lydie	F	Adult	23.12.2001	Amsterdam	
			17.4.2003	Transport to DK	
Lukrecie	F	Young	7.11.2010	Dvůr Králové	
Tootsie	F	Adult	5.10.1995	Dvůr Králové	
Tim	M	Young	3.10.2010	Dvůr Králové	
Tanaka	F	Adult	11.8.2002	Dvůr Králové	
Tanja	F	Young	22.10.2010	Dvůr Králové	
Izabela	F	Young	23.9.2010	Dvůr Králové	

Name	**Sex**	**Age category**	**Birth Date**	**Place of birth**	**Date of loss**
			Date of increment	**Where from**	**How / Where**
Leila	F	Young	16.7.2006	Dvůr Králové	
Ituri	F	Young	1.8.2006	Dvůr Králové	
Bisina	F	Young	29.8.2009	Dvůr Králové	
Jeník	M	Young	22.8.2009	Dvůr Králové	
Jitu	M	Adult	2.2.2003	Frankfurt	
			2.6.2004	Transport to DK	

Appendix 3: Feeding ration in individual zoos

Table 1: Feeding ration in Prague zoo

Type of feed	**Summer**	**Winter**	**Comments**
Bran	0.3 kg	0.3 kg	Mash
Oat flakes	0.3 kg	0.3 kg	
Mashed oat	1.5 kg	1.5 kg	
Pellets Browser	3 kg	3 kg	
Alfalfa pellets	1.5 kg	1.5 kg	
Alfalfa hay	cca 7 kg	cca 7 kg	
Fresh green fodder			
Browse (norway maple, goat willow, sessile oak, cherry tree)	1-2 branches	1-2 branches	
Carrot	1 kg	1 kg	
Cabbage	0.1 kg	0.1 kg	
Apples	1 kg	1 kg	
Onion	0.1 kg	0.1 kg	
Celery	0.5 kg	0.5 kg	
Parsley root	0.5 kg	0.5 kg	

Table 2: Feeding ration in Olomouc zoo

Type of feed	**Summer**	**Winter**	**Comments**
Pellets ZOO A	4.3 kg	4.3 kg	
Alfalfa pellets	1.5 kg	1.5 kg	
Carrot, beetroot, apples	1 - 2 kg	1 - 2 kg	
Alfalfa hay		*ad libitum*	
Green alfalfa	5 kg		
Browse (birch, willow, hornbeam, oak, rowan berry)	1 - 2 branches	1 - 2 branches	
Oat flakes	0.2 kg	0.2 kg	Mash
Linseed extrudate	0.5 kg	0.5 kg	
Wheat bran	0.2 kg	0.2 kg	
Milk powder	0.1 kg	0.1 kg	
Glukopur	0.1 kg	0.1 kg	
Rapass (extruded rapeseed meal)	0.1 kg	0.1 kg	
Feeding limestone	10 g	10 g	

Table 3: Feeding ration in Liberec zoo

Type of feed	**Summer**	**Winter**	**Comments**
Pellets ZOO A	3.5 kg	3.5 kg	
Mzuri	1.5 kg	1.5 kg	
Boskos	0.75 kg	0.75 kg	
Carrot	1.5 kg		
Carrot		1.5 kg	5 times a week
Beetroot		1.5 kg	2 times a week
Alfalfa hay + meadow hay	30 kg	30 kg	
Browse	*ad libitum*	*ad libitum*	

Table 4: Feeding ration in Dvůr Králové zoo

Type of feed	**Summer**	**Winter**	**Comments**
Pellets ZOO A	3.5 kg		
Mzuri	1.5 kg		
Browser Kasper	0.75 kg		
Alfalfa pellets	1.25 kg	0 - 0.63 kg	
Vegetable + Fruit	3 kg	1.5 kg	Vegetable : Fruit in ratio 2 : 1
Carrot	1.5 kg		
Herbs (dried nettle)	*ad libitum*	*ad libitum*	
Vitamix S4 plus	*ad libitum*	*ad libitum*	
Uniruminal	30 g	30 g	
Lactiferm L5	5 g	5 g	
Mineral. lick (minerallecksteine and Mikro Mg Super)	*ad libitum*	*ad libitum*	
Browse	*ad libitum*	*ad libitum*	
Coarse forage		*ad libitum*	
Green fodder (green alfalfa-alfalfa hay and meadow hay)	*ad libitum*		
Oat flakes	250 g	250 g	Mash
Linseed	200 g	200 g	
Wheat bran	250 g	250g	
Milk powder	125 g	125 g	
Herbs (dried nettle)	50 g	50 g	
Glukopur	60 g	60 g	
vitamix S4 plus	50 g	50 g	
Soy flour	60 g	60 g	
Feeding limestone	50 g	50 g	
Oak bark	25 g	25 g	In cases of diarhea only