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Comparison of suckling behaviour among several captive equid species

PhD Thesis

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Synchronized suckling of African wild ass, photo by Jan Pluháček

Suckling and allosuckling of Grevy’s zebra, photo by Jan Pluháček

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Faculty of Tropical AgriSciences

Department of Animal Science and Food Processing Doctoral Thesis I

Research Proposal

Topic of the dissertation **Comparison of suckling behaviour among several captive equid species**

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DECLARATION

Hereby I confirm that I have written my PhD thesis “Comparison of suckling behaviour among several captive equid species”, on my own with a help of literature listed in References. I have provided a complete reference to the resources that are used in this document according to the citation rules of the Faculty of Tropical AgriSciences. All figures and photographs are either by myself or are used with authorisation and quoted author.

In Domažlice 1st April 2022

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Michaela Levá

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VÚŽV
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ABSTRACT

This thesis aims on the comparisons of various aspects of maternal behaviour of the three zebra species: mountain zebras (*Equus zebra*), Grévy's zebras (*Equus grevyi*) and plains zebras (*Equus quagga*). These three species differ in their appearance, ecology and behaviour. My main interest was suckling behaviour. I focused mainly on following characteristics of suckling behaviour: suckling bout duration, suckling bout frequency, the rate of mother's rejections and her terminations, laterality and synchronization. I compared the interspecific differences in these parameters among three zebra species in light of their sociobiology, ecology, and phylogeny. I also observed the adoption and allosuckling behaviour in Grevy's zebra and I compared allosuckling occurrence with two other zebra species as well as with horses. The last topic was zebra's laterality. I examined whether the zebras have any lateral preferences in suckling behaviour, or they are without lateral preference on individual or/and population level. All studies were based on observations at the Dvůr Králové Zoo, Czech Republic. In total, we observed 71 zebras during three years (2008-2010). We found differences in suckling characteristics among all three zebra species. These results show that maternal behaviour is affected by social hierarchy and ecology. In addition, it was found high level of synchronisation in suckling behaviour. Lateral preferences appeared only on individual level in one third of examined pairs. Based on these results, I suggest that future research should aim to other equid species like wild asses and wild horses.

Key words: *allonursing, comparative studies, Equus, laterality, suckling behaviour, synchronisation, zebras*

ABSTRAKT

Tato práce je zaměřena na porovnání různých aspektů mateřského chování tří druhů zeber: zeber horských (*Equus zebra*), zeber Grévyho (*Equus grevyi*) a zeber stepních (*Equus quagga*). Tyto tři druhy se od sebe liší svým vzhledem, ekologií i chováním. Mým hlavním zájmem byla chování týkající se kojení. Zaměřila jsem se hlavně na tyto charakteristiky kojení: délku kojení, frekvenci kojení, míru odmítání a ukončování kojení matkou, lateralitu a synchronizaci. Porovnávali jsme mezidruhové rozdíly těchto parametrů ve světle sociobiologických, ekologických a fylogenetických hypotéz. Mimo jiné jsem pozorovala adopci a pokusy o alokojení u zeber Grévyho a porovnala jsem míru alokojení s ostatními druhy zeber a koňmi. Poslední téma této práce se týkalo laterality u zeber. Zkoumali jsme, jestli mají zebry nějakou stranovou preferenci při kojení, nebo jsou bez stranové preference na individuální a/nebo populační úrovni. Všechny studie byly založeny na pozorování v Zoo Dvůr Králové, ČR. Celkem jsme pozorovali 71 zeber během 3. let (2008–2010). Našli se rozdíly ve všech charakteristikách kojení mezi sledovanými zebrami. Tyto výsledky ukazují, že mateřské chování je ovlivněno sociálním uspořádáním i ekologií. Dále jsem zjistila poměrně častou incidenci synchronizovaného kojení. Stranová preference se vyskytovala pouze u 1/3 zkoumaných párů, a to na individuální úrovni. Na základě těchto výsledků, navrhuji, že by se další studie měly zaměřit na další druhy koňovitých, například divoké osli a koně.

Klíčová slova: *alokojení, Equus, kojení, lateralita, srovnávací studie, synchronizace, zebry*

CONTENTS

1. INTRODUCTION

The research on zebras started in autumn 2008. Then, I was the bachelor student on University of South Bohemia in České Budějovice and I was searching for the topic of my study. I was seeking for any behavioural topic with large mammals. With the help of my roommate Jana, I met my supervisor Jan Pluháček. The coincidence came at the right time as he just started the new project on zebras, therefore my behavioural research could start immediately.

On Saturday 13th September 2008, at 8:00:00 I began my first observation of zebras in the Dvůr Králové Zoo. I observed three nice little Grevy's zebra foals called Belinda, Hedvika, and Kevin. They were just one week old. The first infant – mother interaction appeared very soon, and first successful suckling bout started at 8:19:41 by Belinda. From this moment I collected behavioural data (suckling, resting, grooming, agonistic interactions, and other) in all three zebra species during next two years until the summer 2010. My last observation took place on Sunday 11th July 2010 when I recorded all these behaviours in the group of 13 mountain zebras including 6 foals.

Thus, my dissertation focuses on maternal behaviour of three zebra species: mountain zebras (*Equus zebra*), Grévy's zebras (*Equus grevyi*) and plains zebras (*Equus quagga*). These three species differ not just in their appearance and different stripes. They vary in their behaviour and ecology as well. My interest aimed on mother – infant interactions, especially those associated with lactation in these three species. Lactation is the main form of maternal investment in mammals (Clutton-Brock et al. 1989), being far more energetically demanding than gestation, oestrus behaviour or ovulation (Sadleir 1984; Fischhoff et al. 2007). Moreover, lactation is important not just for the nutrition it provides for offspring, but is also an important component of the mother-infant social and psychological bond.

In spite of the importance of lactation and the fact that behaviour associated with it is easy to observe, suckling behaviour remained an understudied topic in many mammalian species, including zebras (Sadleir 1984; Clutton-Brock et al. 1989; Fischhoff et al. 2007). Although zebras are easily to be observed in the wild, as they remain abundant through most of their range in Africa, and are also common in zoos and safari parks worldwide, the number of studies on their suckling behaviour were limited. In contrast, the suckling behaviour of their sibling species (horses and asses) has been studied in more detail (Cameron, et al. 1999a, b; Cameron & Linklater 2000; Komárková et al. 2011). Therefore, I will refer to this literature when helpful for explanation or when interspecific comparisons provide interesting information.

During my literature study of suckling behaviour of bovids I came across the article about simultaneous suckling in scimitar-horned oryx (*Oryx dammah*) (Drews 1991). During my observations it seemed to me that this phenomenon could be observed in zebra species too. Therefore, I examined the synchronization of suckling behaviour and the results could be found in the first article in this thesis.

We focused on four main characteristics of suckling behaviour: suckling bout duration, suckling bout frequency and the rate of mother's rejections and her terminations. We compared the interspecific differences in these parameters among three zebra species in light of their sociobiology, ecology, and phylogeny. More specific, I was interested how these parameters of suckling behaviour differ among all three species. Becker and Ginsberg (1990) suggested that suckling behaviour reflect adaptation to the natural environment of species. We tested this hypothesis using rejection and termination of suckling bouts in these species, in the perspective of the parent offspring theory (Trivers 1974). We also, compared these characteristics in the view of social and environmental adaptations of these three species.

Another interesting and popular topic in current ethology is allosuckling. I observed these events and allosuckling attempts quite often between Grevy's zebra. In addition, I observed reported the first case of adoption in Grevy's zebra that happened in the orphaned foal Kevin. His mother Šárka died 3rd March 2009 when Kevin was 6- month-old. Fortunately, he started successfully and regularly allosuckle in another mare Tabia who was accompanied by her own foal Belinda. Kevin sometimes allosuckled even in other mares.

The last interesting topic included in this thesis is laterality. Similarly, as allosuckling and synchronisation, the behavioural laterality represents very interesting topic of current sociobiology. Therefore, we tested if the zebras prefer suckling from right or left side either on the population or individual level. Current studies on this topic in equids are scares including just domestic horses. Whereas Carson and Wood-Gush (1983) referred those stabled horses preferred right side for nursing, Komárková and Bartošová (2012) found the laterality on individual level only.

At the end of the introduction, I would like to stress the uniqueness of the studies below as interspecific behavioural comparisons of closely related species are lacking in ungulates and remain rare in mammals in general.

2. AIMS OF THE THESIS

As written in the Introduction, this thesis consists of five various scientific papers dealt with suckling behaviour of all three zebra species. The main aims of this research were as followings:

- Examine if suckling behaviour of zebras is synchronised?
    - If so, the to investigate the effect of synchronisation and especially that of social facilitation in terms of maternal investment and offspring benefit
- Compare interspecific variability in suckling behaviour (especially in suckling bout duration, frequency, rejection, and termination) in three captive zebra species.
    - To find whether these differences are more affected by variability in sociobiology or ecology or are based on phylogenetic relatedness of respective species
- Compare interspecific variability in incidence and characteristics of allonursing behaviour
- Investigate various aspects of laterality associated with suckling behaviour including interspecific comparison

All these aims involved scientific hypotheses based on various theories in behavioural ecology. Specific predictions were formulated to verify the hypotheses. The hypotheses and predictions are included in the respective papers and, therefore were not listed here.

3. REVIEW OF LITERATURE

Zebras

The three extant species of zebra (Grevy's zebra *Equus grevyi*, plains zebra *E. quagga*, and mountain zebra *E. zebra*), together with three species of ass (African wild ass *E. africanus*, Asiatic wild ass *E. hemionus*, and kiang *E. kiang*) and one, horse species (*E. ferus*) belong to the genus *Equus*, the only recent genus of Equidae (Ransom & Kaczensky 2016). Most recent phylogenetic studies agree that zebras and asses are more closely related to each other than to horses (George & Ryder 1986; Oakenfull & Clegg 1998; Oakenfull et al. 2001; Steiner & Ryder 2011; Steiner et al. 2012). Zebras represent a monophyletic group where mountain zebras evolved first, and Grévy's and plains zebra later (thus they are more closely related to each other) (Ryder & Chemnick 1990; Price & Bininda-Emonds 2009).

All three extant zebra species are from Africa. The monotypic Grévy's zebra (*Equus grevyi* Oustalet 1882) is the largest species, weighing around 400kg (Rząśnicki 1951). Formerly found across semi-arid areas of East Africa, the current distribution of Grevy's zebras is limited to northern Kenya and Southern Ethiopia (Estes 1992). Grevy's zebras have a fluid social organization; groups of about 10 females have no fixed membership or hierarchy, with the only long-term bonds being between mares and their most recent 1 or 2 foals. Adult males defend territories of 2 to 11 square kilometres where reproduction takes place almost exclusively (Ginsberg 1988). Therefore, females usually mate with several males as they move across their territories. Gestation period varies between 387-482 days. (Ginsberg 1988; Churcher 1993)

The six subspecies (Groves & Bell 2004) of plains zebra (*Equus quagga*, Boddaert 1785, formerly *Equus burchelli*) inhabit large savannah areas from the Somali-Masai Arid Zone in Kenya and Uganda to the Southern Savanna in South Africa and Angola (Estes 1992). Plain's zebras weigh 175 to 385 kg and are smaller (127–140cm) than Grevy's zebra (Grubb 1981). They live in fixed social groups (harems) of up to 16 animals, consisting of a stallion who has exclusive mating rights with 1 – 6 females, and their foals. Adult females spend almost their whole life in the same harem, where a social hierarchy is well established. Young males form bachelor herds of 3-6 individuals (Klingel 1975). The gestation period of mares is approximately 360 days (Grubb 1981).

Two subspecies of mountain zebra (*Equus zebra* Linnaeus, 1758) inhabit arid mountain ranges parallel to the coast from southern Angola to the Transvaal in South Africa. Mountain zebra are 150cm tall, with a mean weight of 298 kg (Penzhorn 1988).

Similar to the plains zebra they form harem groups, but slightly smaller in numbers (2 – 8 individuals), and bachelor herds consist of yearling females or older stallions that have lost their harems, as well as young males (Joubert 1972; Penzhorn, 1984; Klingel 2010b). Mountain zebra mares are very intolerant towards each other. The hierarchy among females in the harem is much more pronounced than in plains zebra (Lloyd & Rasa 2004), and yearlings are ejected from the group after the mother has a new foal (Joubert 1972). The gestation period in mountain zebras is 362 to 375 days (Penzhorn 1988).

The foals of all three zebra species are followers (Estes 1992), standing up soon after parturition and staying with their mothers until weaning. The most important interspecific difference in the maternal behaviour of zebras is the formation of crèches by lactating Grevy's zebras (Klingel 2010a). The social structure of zebras is very conservative, persisting even in captive or semi-captive conditions, whereas feral asses and horses modify their social organization based on environmental conditions.

Main parameters of suckling behaviour

Although suckling behaviour of equids is easily observed. I follow the standard of most studies, defining a successful suckling bout as lasting at least 5 s. An unsuccessful suckling attempt consists of continuous unsuccessful attempts of a foal to suckle, including a mare's permanent rejection, or contact between the foal and the nipple lasting no longer than 5 s. Interruptions within suckling bouts are considered if lasting from 5 to 60 s (Becker & Ginsberg 1990; Cameron et al. 1999b; Pluháček et al. 2010c).

The five most important behavioural parameters of suckling behaviour include: rate of suckling rejection (attempts rejected by the mare versus successful suckling), initiation of suckling, suckling bout duration, suckling frequency, and suckling bout termination. Several mammalian studies, including meta-analyses, showed that suckling bout duration and frequency is not a good indicator of milk transfer. However suckling rejection and termination are important indicators of conflict over the milk, and suckling bout duration and frequency remain important characteristics of suckling behaviour, because they reflect the amount of maternal care in current offspring (Mendl & Paul 1989; Therrien et al. 2008; Pluháček et al. 2010a,b,c; Bartošová et al. 2011). The importance of suckling bout duration as a measurement of social and psychological needs of offspring has been confirmed in other mammals, e.g., primates (Gomendio 1990).

Suckling initiation

In horses suckling behaviour is almost always initiated by the foal (Tyler 1972). Similarly foals of captive Grévy's, plains, and mountain zebras we observed initiated 99.4%, 99.4% and 98.7% of suckling bouts respectively (Pluháček and Levá, unpublished data). When foals approach their dams to nurse, they often walk along one side of her, push their way under her neck and walk down the other side to the udder. This movement is called "heading-off", and it encourages the mother to stand still (Tyler 1972). "Pushing" the udder with the muzzle is also a common feature of nursing activity which stimulates the release of oxytocin resulting in milk let down (Rashek 1976). This is apparently painful to the mother and she may threaten her infant to discourage it from nursing. Various ways in which females help their offspring to nurse have been described. Horse dams may stand still and flex the leg on the side away from the foal (Tyler 1972), or step forward with their forelegs leaving their hind legs stationary to make the udder more accessible to the foal (Crowell-Davis 1985). Asiatic wild ass dams hold their hind leg away from the body and lift it up while the foal nurses (Rashek, 1964). The occurrence of nursing after a disturbance or after foals have been resting is common (Tyler 1972). Asiatic wild ass and mountain zebra foals have been observed to rouse the mother from lying to allow them to suckle. .

Suckling termination

Mountain zebras terminate suckling in four different ways: moving away, flexion of a hind leg, blocking the nipple with a hind leg, or direct aggression (Penzhorn 1984). In Grévy's zebra, females first try to use a milder form of termination (e.g. moving), later switching to biting or kicking (Rowen 1993). Mares of domestic horses terminated suckling bouts in a similar way to zebras as well as by pawing with the hoof and moving the tail. Moving by the mare is the most common termination behaviour in both zebras and horses. Asiatic wild ass mares were observed to bite in an attempt to terminate suckling (Rashek 1976).

We found interspecific differences in rejection and termination of suckling bouts in all three zebra species kept in captive conditions (Pluháček et al. 2012). We found that mothers of both species originating from an arid environment (mountain and Grevy's zebras) rejected and terminated a lower rate of suckling bouts/attempts than those of plains zebra, which originally came from a mesic environment. Thus, zebra mothers from the arid adapted species seem to be more tolerant of their foals, at least in captive conditions (Pluháček et al. 2012).

Suckling bout duration

The duration of suckling bouts differs among the three zebra species (Pluháček et al. 2014). The longest suckling bouts occur in mountain zebra (in captivity: 71.95 ± 27.64 s (seconds), n = 835 bouts, (Pluháček et al. 2014). Joubert (1972); in the wild: Hartmann zebra *E. z. hartmannae*: 65 to 80 s; Cape Mountain zebra *E. z. zebra*: 90 to 120 s including breaks (Penzhorn 1984). In both subspecies in the wild an interruption (from 5 to 20 s) has been reported after 50-70 s of suckling, which then continues for another 15 s (Pluháček et al. 2010c). Although in captivity I did not observe such an interruption it may consist of what I defined as an attempt after the suckling bout (Pluháček et al. 2011a). In wild Grévy's zebra suckling bout duration ranged from 40 to 70 s (Becker & Ginsberg 1990), similar to our findings in captivity where the average suckling bout lasted 57 s. Plains zebras have the shortest suckling bout duration reported in wild zebras (40 s) (Becker & Ginsberg 1990) and in captivity had an average bout duration of 31 s, (however this study only included one foal) (Prescott 1981). In our sample of 41 plains zebra foals the suckling bout lasted 59.7 s on average. The longest suckling bouts reported lasted 4 minutes 16 s in Grevy's zebra, 4 minutes 35 s in plains zebra, and 3 minutes 14 s in mountain zebra (Pluháček et al. 2014).

In Asiatic wild asses, suckling length varied between 15 and 120 s, decreasing to 50 to 60 s before weaning (Rashek 1976). In horses the suckling bout duration lasts 40 to 90 s (Komárková et al. 2011).

The duration of a suckling bout is most influenced by the animal that terminates it. In all captive zebra species suckling bouts terminated by the foal were longer than those terminated by the mare or by a herdmate. Suckling bouts were shorter when terminated by a herdmate than when terminated by the mare in plains zebra. When considering only suckling bouts terminated by foals, the duration was longest in mountain zebra, followed by plains zebra then Grevy's zebra (Pluháček et al. 2014). Since the interspecific differences were most pronounced in bouts terminated by the foal, the foals of various species differed in their intention of how long to suckle (Pluháček et al. 2014). The effect of termination of suckling bout duration has been reported in many studies on domestic horses (Nicol & Badnell-Waters 2005; Komárková et al. 2011; Bartošová et al. 2011; Komárková & Bartošová 2012).

Both studies comparing zebra species reported different results. Contrasting with the results of Becker and Ginsberg (1990) We documented longer suckling bout duration in plains than in Grevy's zebra. We suggest that this difference could be affected by differences in suckling termination (rate of bouts terminated by the mother).

Suckling bout frequency

In all equid species suckling frequency decreases with the age of the foal. In horses and plains zebras the suckling reflex was observed within 60 minutes after birth, and the first successful suckling occurred within the first two hours. Wild plains zebra foals suckled 12 times within the first four hours (Klingel 1969). In wild Cape Mountain zebra, the frequency of suckling decreased quickly: at four months old foals suckled once every 59 minutes, at 10 months the frequency was once every 135 minutes (Penzhorn 1984). Comparison of suckling bout frequency in all three zebra species in the wild and in captivity found the same pattern. The highest suckling bout frequency was observed in plains zebra followed by mountain zebra, then Grevy's zebra. In captivity, the average suckling frequency per 180 minutes was 3.29 ± 2.14 in Grevy's zebra, 4.68 ± 2.42 in plains zebra and 3.92 ± 2.25 in mountain zebra (Pluháček et al. 2014). The maximum suckling bout frequency per 180 minutes we observed was 17 times in Grevy's zebra, 22 times in plains zebra, and 13 times in mountain zebra. Whereas Becker and Ginsberg (1990) proposed that interspecific differences in suckling frequency and bout duration of zebras are based on adaptation to the environment (arid versus mesic), We suggest that they are more linked with differences in social structure of these species (Pluháček et al. 2014).

Interruptions in suckling bouts

Interruptions, commonly defined as longer than 5 s and shorter than 60 s (Becker & Ginsberg 1990), have been overlooked in many studies on suckling behaviour. A possible explanation for interruptions initiated by the foal is to stimulate nipples, leading to an increased release of oxytocin (Carson & Wood-Gush 1983). While in horses' interruptions are common (up to 65% of all bouts), in zebras they only occur in 10-15% of bouts. The incidence of interruptions within the suckling bout in captive zebras decreases with increasing age of the foal (Pluháček et al. 2010c).

Sociobiology – ultimate factors affecting suckling behaviour

Several sociobiological theories may be applied to explain variability in nursing behaviour in equids. Among these theories the most important is the parent - offspring conflict theory (Trivers 1974). This theory states that, “an offspring attempting from the very beginning to maximize its reproductive success would presumably want more investment than the parent is selected to give”. Conflict with the parent should arise as the foal ages, and can also involve competition between current and future offspring. Such a form of parent-offspring conflict is evident in equids where a nursing mother is pregnant, thus simultaneously investing in two offspring. In the wild, at least half of plains zebra mares conceive when still lactating. Considering parent-offspring conflict theory (Trivers 1974), a pregnant mare should give a lower level of maternal care to a suckling foal than a non-pregnant mare.

Other theories attempted to address the possibility of differential investment in the different sex of the offspring (for a review see (Clutton-Brock 1991). The theory most easily applied to equids is the Trivers-Willard model TWM (Trivers & Willard 1973), which predicts that mothers in polygynous species that are in good condition would increase their fitness by investing more in sons, whereas mothers in poor condition would invest more in daughters. In wild populations the TWM is considered an aspect of sexual selection. In captive conditions ad libitum access to food and water, thus most mares are in good condition and would be expected to invest more in sons than daughters (White et al. 2007).

From these theories, we would expect three main factors to affect maternal investment in terms of nursing: the age of the foal, the sex of the foal and the mare’s pregnancy state, with conflict over resources measured by the mare’s rejection and termination rate, and suckling bout duration and frequency reflecting more maternal care. Before our research on this topic the rejection and termination of suckling had only been studied in horses (Barber & Crowell-Davis 1994), never in zebras. Studies in captive plains zebra (tables 1 and 2) showed an unexpectedly high level of mother-offspring conflict in captive plains zebra (Pluháček et al. 2010c). Mothers frequently rejected and terminated suckling, especially when considering they were in good condition. The level of conflict was a little higher than reported for domestic horses. This indicates that lactation remains very demanding for females (Sadleir 1984), even under captive conditions with balanced nutrition.

Pluháček et al. (2010c) also found an effect of the sex of foal combined with the age of the foal (table 1, 2). Whereas for female foals, the proportion of suckling bouts terminated by the mother decreased with increasing age of the foal, in male foals the proportion of terminations was not related to age (Pluháček et al. 2010c). Thus, the conflict over transferred milk in captive plains zebra decreased with increasing age in female foals only. This suggests that while female foals were satiated with the amount of milk provided by the mother, male foals still required more than what the mother was providing and willing to provide (Redondo et al. 1992). Alternatively male foals may be more persistent and aggressive. Sex dependent differences in suckling behaviour as a non-adaptive trait has been mentioned by several authors for species such as African elephant (*Loxodonta Africana*) (Lee & Moss 1986), red deer (*Cervus elaphus*) (Clutton- rock et al. 1981), and white rhinoceros (*Ceratotherium simum*) (White et al. 2007).

Another explanation is that mothers are more tolerant of their daughters, suggesting differential maternal investment according to the sex of the foal. In wild mountain zebra, high-ranking mothers invested more in daughters (Lloyd & Rasa 2004). As mountain zebras live in an environment where food is scarce, lack of food has a great impact on mare reproductive success (Lloyd & Rasa 2004). In feral domestic horses' mothers in good condition terminated and rejected more suckling bouts/attempts for daughters than sons, whereas mothers in poor condition terminated and rejected more suckling bouts/attempts for sons than daughters (Cameron & Linklater 2000). These findings suggest that equid mothers alter investment in their offspring depending on available resources, sex-biased differences in reproductive potential, and the social organisation of different species.

To solve the question of whether it is the foal or mare that is more responsible for sex dependent variability in suckling rejection and termination Pluháček et al. (2011a) performed another study measuring the occurrence of subsequent attempts and the length of interruptions in captive plains zebra. They found that whereas in female foals the probability of a subsequent suckling attempt decreased with increasing age of the foal, in male foals the probability of a subsequent attempt did not change with increasing age. In addition, male foals resumed interrupted suckling bouts sooner and had more subsequent attempts than female foals. We did not find any differences between the sexes in suckling bout duration and frequency. As suckling bout frequency and duration reflects maternal care but not maternal investment, the mother of captive plains zebra did not differentiate their care and investment according the sex of their offspring. These results support a hypothesis that the sex dependent differences in suckling behaviour result from different behaviour of the young rather than different investment by the mother (Pluháček et al. 2011a). These findings also highlight the importance of studying the length of the interruption of a suckling bout and subsequent attempts to suckle. Therefore, these characteristics should be considered in future studies on suckling behaviour in captive equids.

The age of the foal affects many aspects of suckling behaviour, in addition to its effect on suckling bout termination and rejection. The frequency of suckling decreases sharply with increasing age of the foal across all equid species, and suckling bout duration decreases with increasing age of the foal in most species, although this effect was not observed in two reports on horses and wild plains zebra. The first few weeks of life are the most critical period for lactation as foals rely almost entirely on maternal milk for resource acquisition, but since suckling bout duration is correlated with non-nutritive demands of the foal, the decline in frequency and duration reflects a reduction in intensity of contact with the mother as the foal grows up. It showed that the probability of suckling bouts being interrupted decreased with increasing age of the foal in captive plains zebra, implying that suckling skills improve in zebra foals as they grow older (Pluháček et al. 2010c).

These studies remain unique in looking for the effect of pregnancy on zebra suckling behaviour. They did not find statistically significant differences in rejection or termination between pregnant and non-pregnant mares (Pluháček et al. 2010a). Since the effect of pregnancy on maternal behaviour has been reported in other feral and wild equid populations, they suggest that captive conditions with unlimited resources help mares to cope better with investment in two offspring (foetus and suckling foal) at the same time. On the other hand, they observed that nursing bouts of pregnant mares were shorter than those of non-pregnant mares (Pluháček et al. 2010a). The effect of pregnancy was also found when only considering bouts terminated by the mother. This might indicate a little lower maternal care in pregnant mares compared to non-pregnant mares. However, the difference was small, and since a recent study on domestic horses found opposite results (Bartošová et al. 2011). They cannot make any strong conclusions about the effect of pregnancy on suckling behaviour in captive zebras. It remains clear, at least from behavioural observations, that pregnancy during lactation under captive conditions is not a handicap and mares could be allowed to become pregnant again without any deleterious effect to the current or subsequent offspring.

One of the most important factors affecting various behavioural traits is social hierarchy and networks. Among equid societies harassment and interventions have been reported to be an important feature of nursing. In wild-living mountain zebras and certain populations of feral domestic horses “dominant mares aggressively interrupt suckling bouts between subordinate mares and their foals by biting and chasing the mother, thus delaying the foal's milk intake" (Lloyd & Rasa 2004). In the study on captive plains zebra (Pluháček et al. 2010c), they found that dominant mares interrupted and terminated suckling bouts of other mares more often than subordinate mares, however the overall number of suckling bouts and attempts terminated by other mares was very low (table 1 – 3). Therefore, the effect of herdmates on suckling behaviour in captive zebras is very low. Moreover, we detected that the probability that the foal resumed suckling after an interruption caused by a herdmate was almost six times higher (47%) than when the interruption was caused by the mother or foal (8%). If the interruption/termination of the suckling bout was caused by a herdmate, older foals resumed suckling more often than younger ones. The negligible effect of other mares on suckling behaviour has been further reported by detailed studies on domestic horses. Thus, based on the published results of suckling behaviour, the separation of zebra mothers with their foal as a prevention of harassment by other mares is not recommended. Nevertheless, it should be stressed that in captive mountain zebra the separation of adult individuals in stables is necessary to prevent injuries due to other reasons, and that in Grevy's zebra forming a separated group of mares with foals is appropriate as it is similar to the social organization known from the wild. However, these recommendations do not emerge from our knowledge of maternal behaviour but from other aspects of zebra social behaviour.

Proximate factors affecting suckling behaviour

In many mammalian species environmental conditions affects offspring development as much as time before weaning (Bateson 1994). However, most current research is focused on the effect of sociobiological factors on suckling behaviour, overlooking proximate environmental factors such as feeding during suckling, and where it occurs (enclosure versus stable, the design of stable/enclosure).

Free-ranging equids feed for a rather constant 59–69% of the day. In feral horses the proportion of suckling bouts during which mares continued to graze gradually decreased with increasing age of the foal (Tyler 1972). In both wild and captive plains zebra, females spent more time foraging than males (Schilder & Boer 1987). Captive plains zebra mares and domestic horses spent less time feeding in grassless enclosures than when on pasture (Andersen 1992). Thus, enclosure design as much as feeding schedule can affect behaviour, including suckling.

We studied the effect of feeding on suckling behaviour in all three captive zebra species in stables and in enclosures where no grass was present and all food was provided in feeders, examining impact on suckling bout rejection, termination, duration, and interruption. When the mare was feeding as the foal began to suckle there was a lower probability of refusing the suckling attempt (56 %, N = 2662) than when she was not feeding (67 %, N = 4885) (Pluháček et al. 2012). When the mother was feeding while nursing the proportion of suckling bouts terminated by her decreased with increasing age of the foal. When the mother interrupted feeding during the suckling bout, she terminated the bout more often compared to when feeding continuously (Pluháček et al. 2010b).

Suckling bouts lasted longer when the mother interrupted feeding due to nursing than when the mother did not feed or when she was feeding during the whole bout. In addition, when she was not feeding the suckling bout duration was longer than when she was feeding while nursing (Pluháček et al. 2014). The suckling bout was interrupted more often when the mother was feeding while nursing than when she was not feeding (Pluháček et al. 2010b). This indicates that when the mother herself was feeding, the suckling process proceeded better for the foal.

On the other hand, suckling behaviour also affects feeding behaviour of the mother when suckling starts while she is at the feeder. Interruption of feeding of the mother while nursing increased with increasing age of the foal, and with decreasing age of the mother (Pluháček et al. 2010b).

Our research confirmed that feeding while suckling reduces parent-offspring conflict (Trivers 1974) in terms of lower proportion of bouts terminated by the mother. Therefore, ad libitum feeding is not just necessary for nutrition of the mother, but also improves welfare of captive foals. This is in agreement with other studies suggesting the importance of ad-libitum and/or multiple feeding locations for improving welfare of captive equids (Doreau et al. 1978; Thorne et al. 2005; Goodwin et al. 2007).

Weaning

Weaning is a critical process in mammalian parental care (Counsilman & Lim 1985). As a lot of confusions associated with weaning are caused by missing definitions, it is necessary to clarify various types. In general, three types of weaning can be distinguished (Martin 1984a). First, metabolic weaning is the period when offspring separated from the mother will survive without any damage in terms of physiology (Martin 1984a). It should be noted that psychological necessities are not mentioned in this type of weaning. Second, artificial behavioural weaning is the process directly affected by humans, i.e., the offspring is forcibly separated from the mother (Weary et al. 2008). Third, natural behavioural weaning is the process without human intervention where a major role is played by the mother and her offspring. In most species metabolic weaning precedes the time of natural weaning which demonstrates clearly that the later stages of lactation are important psychologically rather than for nutritive value (Joubert 1972).

Both artificial and natural weaning can be an abrupt or gradual process. Abrupt artificial weaning means complete separation in time and place without any further contact between mother and offspring (Apter & Householder 1996). Gradual artificial weaning occurs when the mother is separated from her offspring by a barrier, so nursing is not allowed, but the visual, acoustic, and olfactory contacts remain. Nevertheless, in all cases artificial weaning means sudden and mostly irreversible termination of the nursing process. Abrupt natural weaning occurs when either the mother suddenly restricts suckling by her offspring, or the offspring voluntarily leaves the mother (e.g., tree shrews *Tupaia*) Gradual natural weaning is a slow process leading to the termination of lactation (most mammals including rodents, bats, and artiodactyls) (Pond 1977; Martin 1984b; Lee et al. 2009). Although these definitions seem to be trivial, some high-quality scientific papers overlooked artificial weaning as an explanation in natural situations.

One of the best ways to improve welfare in a captive environment is to prefer natural weaning to artificial. Therefore, knowledge of natural maternal behaviour has crucial welfare implications. Moreover, this knowledge gives also important information about the investment of a mare in her offspring.

Similar to the suckling process, natural weaning could be affected by a number of factors. However, very few studies have examined the effect of any factor on natural weaning except the age of the offspring. One of the main factors that can affect the length of lactation in mammalian species, especially in those where the lactating female conceives shortly after birth is subsequent pregnancy (Bateson 1994).

Depending on the environmental conditions, the optimum weaning time should occur earlier for pregnant than for non-pregnant females (Bateson 1994). This has been documented for various ungulates, such as Saharan arrui (*Ammotragus lervia*) (Cassinello 2010) and American bison (*Bison bison*) (Green et al. 1993). In African elephants (*Loxodonta africana*) the duration of maternal investment via nursing appeared to be controlled by the inter-birth interval of the mother (Lee & Moss 1986).

Various equid studies have shown the age of the foal at weaning but few of these researchers analysed factors that could influence the weaning age. In mountain zebra, Asiatic wild asses and horses, pregnant mares nurse their foals for a shorter period than the non-pregnant dams. In contrast to these findings, one study of feral horses revealed that older mothers (over 9 years of age) did not significantly differ in foal weaning age in relation to their reproductive condition (Cameron et al. 2000). These mares generally weaned their foals before 1 year of age, regardless of whether or not they were pregnant, whereas younger mothers continued to suckle their yearling offspring in the next breeding season if they did not have a subsequent pregnancy (Cameron et al. 2000). In feral horses the duration of lactation lasted longer for primiparous than for multiparous feral horse mares (Duncan et al. 1984), there was no difference in weaning age between male and female foals, and weaning dates did not vary in relation to the condition of the mare (Cameron & Linklater 2000) or by the number of stallions in a group (Cameron et al. 2009).

The reports on age of the foal at natural weaning in wild zebra species produce more varied results. King (2008) reported weaning to occur at 7 and 9 months of age in plains and Grévy's zebra respectively in East Africa; 25 years later, Becker and Ginsberg (1990) reported opposite results: 15.5 (±2.2) months (n = 7) in plains zebra and 11.8 (± 0.8) months (n = 32) in Grévy's zebra. Smuts (1976) observed that weaning occurred between 9 and 16 ("normally 11") months in plains zebra in South Africa. Wild mountain zebra weaned their foals when around the age of 10 months and at least 2 months before the next parturition. Penzhorn (1979) reported cases of orphans at the age of 7 months. Thus, in mountain zebra the fact that the metabolic weaning precedes natural weaning has been clearly documented. None of these studies considered any factor influencing weaning time except age of the foal.

In our study on captive plains zebra at Dvůr Králové Zoo (Czech Republic) We documented natural weaning for 10 foals and artificial weaning for 6 foals. We found that natural weaning was abrupt: from one week to the next the mother went from nursing normally to no further suckling being observed. Three main factors affected natural weaning in plains zebras: the age of the foal, the pregnancy state of the mother, and the sex of the foetus in pregnant mothers. The earliest weaning, we recorded occurred was a (male) foal at only 8 months (243 days) old. His mother gave birth to the next offspring 160 days later. The earliest weaning of a female foal was at 284 days old. The average age of the naturally weaned captive plains zebra foals was 11 months (327 ± 61 days). By comparison, in feral horses, the youngest weaned foal was 140 (Duncan et al. 1984), 143 (Zwoliński & Siudziński 1966) or 196 (Cameron et al. 2000), days old, and 236 days in Asiatic wild ass (Rashek 1976), thus earlier than zebras.

Pregnant captive plains zebra as well as wild mountain zebra mares weaned their foals sooner than non-pregnant mothers (Pluháček et al. 2007). They observed two individual mares wean foals while pregnant and non-pregnant, one of them produced only male foals and the other female foals. When pregnant, they weaned their foals more than

50 days earlier than when they were non-pregnant. The latest suckling, their recordings occurred 83 days before the next delivery, when the (female) foal was at the age of 355 days. As all weaning cases of non-pregnant mares were artificial, the variation in weaning time between pregnant and non-pregnant mares could in fact be much greater. Similarly non-pregnant mares of wild mountain zebra were observed to nurse their foals up to 20 months of age (Penzhorn 1984). The time to delivery in captive plains zebra varied from 83 to 185 days (138 ± 34 days). These values are within the range reported for feral horses (21-161 days, mean 105 days) (Duncan et al. 1984). Therefore, the interspecific differences in weaning age among horses, Asiatic asses, plains and mountain zebras could be based on differences in their gestation periods. Under optimal conditions, mares mate shortly post-partum and the inter-birth intervals differ due to different gestation period lengths. This might be the main reason why horses and Asiatic wild asses wean their offspring sooner than zebras.

The third important factor affecting natural weaning in captive plains zebra was the sex of the foetus. If the foetus was male, then the mare was more likely to wean her current suckling offspring earlier than if the foetus was female (Pluháček et al. 2007). This may be due to preferential investment in male offspring compared to female offspring during the time when the foetus is completely dependent on maternal investment. Thus, captive plains zebra mares appear to be changing the length of time between weaning and delivery of the next foal, suggesting they might be trading off a value of current and future offspring.

Neither our study in plains zebra nor studies examining horses revealed any effect of sex of the weaned foal. Nevertheless, it should be noted that at least in our study, the sample size was very limited. Similarly, the weaning process did not influence the mortality rate of new born foals. This result is important as it suggests that mortality of new born zebra foals at a zoo is probably not caused by nutritional stress, since plentiful resources were available. The implications for welfare of captive zebras are therefore: (1) not to artificially wean foals before the period of natural weaning (10 months in all three zebra species); and (2) artificial weaning does not prevent mortality, as the weaning process did not affect survival of subsequent offspring.

Allosuckling and adoption

Allosuckling is when a female mammal nurse's offspring that are not her own (Lewandrowski & Hurnik 1983). Packer et al. (1992) summarized allosuckling among many mammalian species, revealing a high incidence in carnivores, primates, and rodents.

Allosuckling has been recorded more often in captive environments than in the wild (Packer et al. 1992) due to access to unlimited food and limited space, which may provide females with sufficient nutrition, but preclude them from successfully avoiding non-filial offspring attempting to suckle. In ungulates allosuckling is much more common among artiodactyls than in perissodactyls (Packer et al. 1992; Zapata et al. 2009, 2010; Brandlová et al. 2013).

The function of allosuckling for females remains a question. Roulin (2002) summarized all known hypotheses explaining why allosuckling happens in various mammalian species: (i) the misdirected parental care hypothesis, (ii) the reciprocity hypothesis, (iii) the kin selection hypothesis, (iv) the milk evacuation hypothesis, and (v) the parenting hypothesis. The hypotheses supported most often by emprical evidence are the misdirected parental care and the kin selection hypotheses (Cameron et al. 1999a).

On the other hand, allosuckling could be seen as advantageous for young. A commonly accepted hypothesis is that allosuckling provides extra energy (Packer et al. 1992); Víchová and Bartoš (2005) proposed a compensation hypothesis. Roulin and Heeb (2002) suggested that allosuckling young can have an immunological advantage, as it improves their resistance against pathogens and parasites, although the converse has also been shown.

Allosuckling as a part of adoption in zebras and horses

Allosuckling is a very rare event in equids, being associated with adoption in all observations except Grévy’s zebras (Olléová et al. 2012). The first case of allosuckling recorded in equids was documented by Rashek (1964) in a wild population of Asiatic wild ass (*E. h. kulan*). The mother of a foal (of unknown age) was pursued by a stallion over a long distance, resulting in the foal being left with the rest of the herd. The foal was adopted by another mare, who nursed it with her own foal. The next day when the mother returned, the adoptive mother refused to return her foal. It was subsequently separated by human intervention.

In wild mountain zebra, a newborn foal was adopted by another mare with her 4-week-old foal in the same breeding herd (Lloyd & Harper 1980). Penzhorn (1984) recorded the adoption of a 10-week-old wild mountain zebra foal by another mare in the herd which nursed it with her own 2-month-old foal. The adopted foal disappeared from the herd at the age of 8 months.

One case of adoption was seen in captive Somali wild ass (Lang 1972): a foal was orphaned at the age of 5 months and subsequently adopted by another mare with her own 4-month-old offspring. Both foals were raised successfully to adulthood.

Cameron et al. (1999a) observed one feral horse foal out of 113 being nursed by two mares, a mother and daughter. Both mares were pregnant, but after parturition were seen with just one foal. The mares shared nursing and rearing of the foal equally. This foal was raised successfully, unlike many other orphaned foals observed by the same researchers (Cameron et al. 1999a).

Pluháček et al. (2011b) observed an orphaned captive plains zebra male foal allosuckling from one female. The foal was orphaned at the age of 9 days, 3 days after a female from the herd had given birth. The mare nursed the orphan together with her own female foal. There was no difference in duration of suckling bouts between the filial and adopted foal. The suckling bout duration of these two foals was shorter than suckling bouts of other foals in the herd. Both foals successfully grew to adulthood. A plains zebra foal orphaned in the same herd at the age of 5 months was never observed to nurse from another mare in the herd.

I recorded one case of adoption of a captive Grevy's zebra foal (Olléová et al. 2012). The foal's mother died when he was 6 months old, and within a week he was nursed by another mare with her own 6-month-old female foal. The mare did not restrict milk intake to her filial foal. Both the filial and adopted foal were successfully raised to adulthood. The orphan attempted to suckle more often and allosuckled more frequently than all filial foals in the herd, and his suckling bouts were shorter in duration. I suggest that adoption in Grevy's zebra was facilitated by the different social system of this species, and resulting higher tolerance of mares towards non-filial offspring (Olléová et al. 2012).

Allosuckling without adoption

In spite of many studies involving long-term observations of maternal behaviour of domestic and feral horses, only a few cases of attempts to allosuckle have been recorded (Stanley & Shultz 2012).

Attempts to allosuckle in captive mountain and plains zebra foals were very rare in our observations; representing less than 0.2 % of all records (Olléová et al. 2012). In contrast, Grevy's zebra foals attempted and succeeded in allosuckling more often; more than half of all observed foals succeeded at least once (Olléová et al. 2012), and none of these cases involved adoption. As with adoption cases, it appears that the social organization of females could be an important factor affecting the incidence of allosuckling in zebras, because Grevy's zebra mares were more tolerant to nonfilial foals than plains and mountains zebra mares (Olléová et al. 2012).

Practical implications

Based on the current knowledge of maternal behaviour of zebras, adoption could be considered when a foal is orphaned. Current evidence indicates that adoption would be easiest in Grevy's zebras, and less likely in mountain zebras. However, as adoption cases are so rare in equids much will depend on the individual situation. We recommend performing the introduction of an orphaned foal as soon as possible after the parturition of another mare. In all cases the introduction should be very careful with detailed monitoring of the situation over several weeks even if successful adoption occurs.

Welfare implications and conclusions

In this chapter I attempted to summarize the current knowledge on factors affecting suckling behaviours associated with conflict over milk (rejection and termination), maternal care (duration and frequency of suckling), weaning, and allosuckling. As we showed, these behaviours vary according to the species, the age and the sex of the foal, the age and pregnancy of the mother, and environmental factors.

Based on the current knowledge of suckling behaviour of zebras we suggest several ways to improve welfare of these animals in captivity:

1. Separation of the nursing mother and her offspring from the herd is not recommended unless there is a direct attack on the mother. Similarly, the stallion should remain within the herd as he does not disturb maternal behaviour.
2. The social composition of the herd should reflect the social structure of the respective zebra species as documented in the wild.
3. Longer and / or frequently occurring suckling bouts do not reflect a higher maternal investment but rather a higher social need and/or stress of the foal. However, it should be taken into account that long and frequent suckling bouts in mountain zebra and in young foals of all equids seem to be natural.
4. The conflict over resources between zebra mothers and foals could be measured by maternal rejection and bout termination rate. Frequent rejection and termination by a mare indicate nursing is a burden for her.
5. Providing food in more places within a grassless enclosure would reduce conflict between feeding and nursing behaviour of the mother for mountain and plains zebras.
6. Natural weaning should be preferred. As data are still sparse on an exact age, foals of all zebra species should not be separated from their mother when younger than 10 months old. Since natural weaning has no effect on mortality of subsequent

offspring, early weaning should not be used as a reason for “increasing production of foals”.

7. Allonursing is an extremely rare event in all equids. On the other hand, adoption has been observed and could be considered by introducing an orphaned foal to another mare from the same herd with a new-born foal. In all cases, the situation must be checked carefully and individual variability should be considered.

Despite the progression in research on the maternal behaviour of zebras over the last few years, there are still some understudied areas that were studied in horses and asses. We therefore included relevant studies on other equids in this chapter. However, it would be advantageous if more horse studies included research on closely related species like zebras. Welfare of captive animals cannot be improved without knowledge of the basic biology of each species. Although we studied zebras in a zoo environment at the 3rd to the 6th generation in captivity, they remain shy and retain a social life comparable to their wild counterparts. Therefore, I hope that the knowledge on suckling and associated behaviour of wild and captive zebras summarized in this chapter can contribute to improving the welfare of zebras as well as their close relatives: asses and horses.

4. MATERIALS AND METHODS

Materials and methods including all details about animals as well as statistics are described in individual papers. Therefore, this chapter include just brief summary for better orientation.

All studies are based on observations of three zebra species that were carry out at the Dvůr Králové Zoo, Czech Republic. In total, I observed 43 mares and 28 foals during three years (2008-2010). More specifically I researched 19 mares and 14 foals of plains zebras, 10 mares and 6 foals of mountain zebras, and 18 mares and 8 foals of Grévy's zebras were included. Altogether, 795 hours during 140 days were spent by the observation. In addition, data from observation on plains zebra (14 mares 27 foals) at the same zoo carried out by Jan Pluháček in 1999-2002 (831 hours, 159 days) were included to all analyses. The methods in both these observation periods were identical in each detail.

All additional data on animals were received from the Dvůr Králové Zoo and respective studbooks.

The details on animal management and housing system were described in detail by (Pluháček 2017). It should be stressed out that most enclosures, group size, and housing system were very similar. This represents unique opportunity for interspecific comparison. All statistical analyses were performed in SAS/STAT® software, versions 9.2-9.4. Mostly GLMM or logistical regression (procedure GENMOD in SAS) were used to analyse the data based on characteristics of variables. I would like to emphasize that in all models the identity of the individual was used as a subject in the repeated statement to avoid repeated measures on the same individuals across the period of observation. Detailed analyses can be found in each paper.

5. ARTICLES

1. Does social facilitation affect suckling behaviour in zebras?

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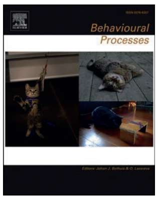

Does social facilitation affect suckling behaviour in zebras?

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ABSTRACT

Many recent studies show that synchronisation of various behaviours are advantageous for group-living mammals. However, studies on synchronisation of suckling behaviour inmonotocous species are nearly absent. We observed 49 individual foals of three zebra species in Dvůr Králové Zoo, and recorded a total of 5 890 suckling bouts, almost one fifth (1 036) of which were synchronised (defined as at least two bouts overlapping at the same time). We found that synchronised suckling bouts lasted longer and were less likely to be terminated by the mother than non-synchronised ones. This is in line with social facilitation theory. In addition the occurrence of synchronised suckling bout differed interspecifically. In plains (*Equus quagga*) and mountain zebra (*E. zebra*) the probability of synchronised bouts increased with increasing numbers of foals, whereas the opposite result was found in Grevy's zebra (*E. grevyi*). We suggest that the interspecific differences may reflect differences in social organisation of respective species as suckling synchronisation rate was higher in species that form nurseries in the wild.

1. Introduction

Synchronised behaviour is advantageous among mammals (Šárová et al., 2007; Stoye et al., 2012), especially those living in long term social groups (Austin and Rogers, 2014; Krause and Ruxton, 2002; Pays et al., 2012; Sirot and Touzalin, 2009). It has been reported that group members are faster at finding good pastures or coordinate antipredator scans more efficiently (Rodríguez-Gironés and Vásquez, 2002) because each individual of the group tends to copy the food intake and movements (Dindo et al., 2009; Wechsler and Brodmann, 1996). Researchers have mostly studied the synchronisation of reproduction of animals (Holt et al., 2020; Pope et al., 1991; Skinner et al., 2002), synchronisation of resting behaviour (Michelena et al., 2008; Šárová et al., 2007; Stoye et al., 2012), synchronisation of movement (Couzin et al., 2002; Michelena et al., 2008; Šárová et al., 2007), or the synchronisation of herd vigilance (Öst and Tierala, 2011; Sirot and Touzalin, 2009).

Although recent studies on synchronisation of other behaviours, such as food intake, remain scarce, it was documented in the past that animals will eat more of their food if there are others of their species present (Zajonc, 1965; Platt et al., 1967). This is in line with social facilitation theory (Triplett, 1898; Zajonc, 1965). Social facilitation can be defined as an increase in the frequency or intensity of responses, or initiation of particular responses, already in an animal's repertoire, when shown in the presence of others engaged in the same behaviour (Triplett, 1898; Zajonc, 1965; Zajonc et al., 1969). Two types of social facilitation can be distinguished: audience effect and co-action effect (Zajonc, 1965). Audience effect can be explained as considerable improvement in performance through observing other individuals engaged in such tasks. Co-action effects occur when an individual simultaneously engages in the same activity and in full view as others do (Zajonc, 1965).

Whereas synchronisation of suckling behaviour has been studied intensively among polytocous species (Maletínská and Špinka, 2001; Wechsler and Brodmann, 1996), studies in monotocous species are lacking. To our knowledge, only one such study was performed on captive scimitar-horned oryx (*Oryx dammah*) (Drews, 1991) using a limited sample size (3 mother-offspring pairs). In this species, the suckling bout duration lasted much longer when they were synchronised, than when the suckling bouts were not synchronised.

The three extant zebra species differ in their social systems (Klingel, 1975; Rubenstein, 1989). Grevy's zebra (*Equus grevyi*) have an extremely fluid social organisation without group membership or a hierarchy, however mares with young foals of the same age create

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nurseries for up to 6 months (Ginsberg, 1988; Rowen, 1993; Rubenstein, 1989). On the other hand, plains zebra (*E. quagga*) and mountain zebra (*E. zebra*) live in fixed social groups with long-term bonds (Klingel, 1967; Penzhorn, 1984). Since reproduction of all zebra species is not seasonal (foals are born year-around with small peaks in summer or wet seasons), (Ginsberg and Rubenstein, 1990; Joubert, 1974; Penzhorn, 1984; Rubenstein, 1989), the foals of Grevy's zebra are more likely to socialise with other foals of the same age than the foals of the other two species. Since differences in social organisation affect maternal style, including suckling behaviour, in various species such as macaques (Maestripieri, 1994), voles (McGuire et al., 2011), and zebras (Olléová et al., 2012; Pluháček et al., 2014), we presumed that the occurrence of synchronisation in suckling behaviour could be affected by the different social organisation of the individual zebra species.

In this study, we examined whether synchronisation influenced suckling bout duration and termination in all three zebra species in captivity. Furthermore, we focused on interspecific differences in the synchronisation of suckling behaviour among zebra species. Based on previous findings, we tested the following predictions: (1) synchronised suckling bout duration lasts longer than non-synchronised suckling bouts; (2) synchronised suckling bouts are terminated less frequently by the mother than non-synchronised suckling bouts. In addition, we also compared the effect of synchronisation on suckling bout duration and termination between the foal that started to suckle first and the foal that suckled second. Lastly, we predicted that (3) synchronised suckling bouts occur more often in the species that creates nurseries (Grevy's zebra) than in the other two species.

2. Material and methods

2.1. Animals

In total, we observed 49 individual foals and 34 adult females of three zebra species (35 plains zebra, 8 Grevy's zebra, and 6 mountain zebra) that were split into 5 different groups in Dvůr Králové zoo, Czech Republic. Plains zebra were observed from January 1999 to January 2000 and from September 2001 to March 2002. All three species were observed from September 2008 to July 2010. Each observation session lasted for 180 min (started either from 8h00 or 14h00). In total, we undertook 1 344 h (448 sessions during 280 days) of observations.

We collected all data concerning any suckling event during each observation. We used the same definitions of suckling bout, suckling attempt and interruption of suckling bouts as described in previous studies on equids (Becker and Ginsberg, 1990; Cameron et al., 1999a; Ginsberg and Rubenstein, 1990; Pluháček et al., 2010a). A suckling bout was regarded as successful when it lasted longer than five seconds and was not interrupted for longer than 60 s. If the interruption of a suckling bout was longer than 60 s, it was considered two suckling bouts. Suckling attempts were defined when suckling lasting less than five seconds or when foals approached their mothers and the mothers walked away or did not allow the foals to make contact with the teats. We recorded the following data for each suckling bout or suckling attempt: the foal's and mother's identities; the animal that initiated (foal or mother), terminated or interrupted (foal, mother, other herdmate or disturbance by people [further referred to as "disturbance" only]) a suckling bout; the duration of the bout (in seconds); and the length of interruption within a suckling bout (from five to 60 s). We defined three types of synchronised suckling bouts as following. "Synchronised bouts" involved all cases where at least two bouts overlapped for at least several seconds at a time, irrespective of which foal started suckling ("simultaneous suckling" in Drews, 1991). We divided these bouts into two types. When the first foal started to suckle the bout was labelled as a "synchronised suckling bout by initial foal" and when the second foal started to suckle during suckling by the first one then the bout was called a "synchronised suckling bout by second foal". All other data concerning the animals (i.e. date of birth of the foals and parents, number of previous foals of the mother, etc.) were obtained from curators of the zoo. Suckling bouts terminated by a herdmate or disturbance, as well as those involving mares other than the mother, were excluded from these analyses. In addition, we did not include observations when only one foal was present in the group.

2.2. Statistics

We analysed the data using SAS/STAT® software, Version 9.4. Suckling bout duration and synchronisation factors influencing the suckling bout duration were tested using a multivariate general linear mixed model (GLMM, PROC MIXED, SAS). The fixed factors (independent variables) tested in all models were synchronisation (yes/no), species, the foal's age (Grevy's zebra 5–395 days; plains zebra 0–394 days, mountain zebra 0–397 days) and sex, the group nested within the season (1999/2000, 2001/2002, 2008/2010), the age of the mother (3–21 years), her parity, her pregnancy (yes/no), the number of other suckling foals within the group (1–7), the number of other animals in the group (1–25), the number of previous births of the mother (0–14), the number of offspring successfully reared by the mother (0–11), the place where the suckling bout occurred (stable/enclosure), who terminated the suckling bout (mother/foal) and the feeding status of the mother ("yes"/ "no"/ "interrupted due to nursing"), and their first-order interaction terms.

The effect of synchronisation on suckling bout termination was analysed using logistic regression (the GENMOD procedure in SAS). We tested the probability that the mother terminated the suckling bout. Independent variables were synchronisation, species, the foal's age and sex, the group nested within the season, the age of the mother, her parity, her pregnancy, the place where the suckling bout occurred, the feeding status of the mother, and their first-order interaction terms.

Both these analyses (suckling bout duration and suckling bout termination) were performed in three separate ways including either synchronisation or initial synchronisation or following synchronisation among the explanatory variables.

The occurrence of synchronised suckling bouts

To compare the occurrence of synchronised suckling bouts interspecifically, we applied logistic regression (GENMOD, SAS). The GENMOD procedure was designed for the probability that suckling bouts are synchronised. As the number of foals varied highly among different groups and species, we included among the explanatory variables species, interaction between species, and the number of other suckling foals in the group (further referred to as "number of other foals"). Besides this, the model contained other explanatory variables, such as the age and the sex of the foal, species, the age and the pregnancy status of the mother, feeding status of the mother while suckling, the time of the day when the suckling bout occurred, if the foal rested before the bout (yes/no) and the place where the suckling bout was performed.

In all models repeated measures on the same individuals across the period of observation were handled with the individual foal 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. The differences between the means were tested using a t – test with multiple comparisons; we used the Tukey–Kramer adjustment.

3. Results

In total, we recorded 5 890 successful suckling bouts. Almost one-fifth (1 036) of all suckling bouts were synchronised (Table 1).

3.1. The occurrence of synchronised bouts

We found that the occurrence of synchronised bouts was affected by the number of other foals ($F_1 = 6.82$; $P < 0.01$), the interaction between species and number of other foals ($F_2 = 8.61$; $P = 0.014$; Fig. 1), the

Table 1

Degree of suckling synchronisation in three zebra species.

Type of synchronisation	Synchronized bouts[a]		Initially synchronised bouts[b]		Followed synchronised bouts[c]	
Species	Yes	No	Yes	No	Yes	No
Grevy's zebra	282 (20%)	1 101	150 (11%)	1 233	150 (11%)	1 233
Mountain zebra	219 (27%)	596	117 (14%)	698	117 (14%)	698
Plains zebra	535 (14%)	3 157	277 (8%)	3 413	278 (8%)	3 414
Total	1 036 (18%)	4 854	546 (9%)	5 346	545 (9%)	5 345

[a] Synchronised bouts involved all cases where at least two bouts of two different foals overlapped for at least several seconds at a time, irrespective of which foal started suckling first.

[b] Initially synchronised bouts occurred when a foal started suckling its mother and during this suckling bout, any other foal started suckling its own mother, too.

[c] Followed synchronised bouts occurred when a foal started suckling after any other foal in the herd has just been performing suckling.

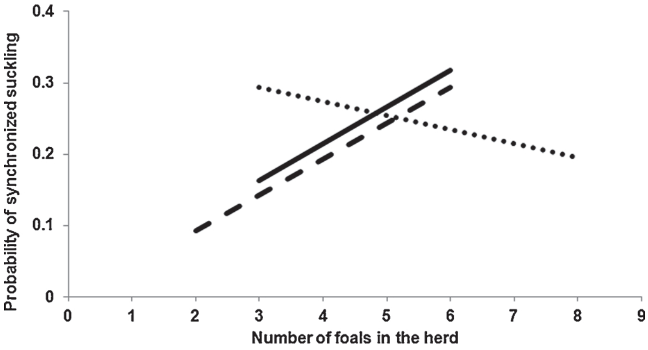

Fig. 1. Interspecific comparison for the probability that suckling bout is synchronised according to the number of foals in the group and the zebra species. Dotted, full, and dashed line represents Grevy's, mountain, and plains zebra, respectively.

place where suckling was performed ($F_1 = 8.54$; $P < 0.01$) and the age of the foal ($F_1 = 9.84$; $P < 0.01$). Whereas, in plains and mountain zebra the probability of synchronised suckling bouts increased with an increasing number of foals within the band at that time, with no difference between these two species, the opposite was found in Grevy's zebra (Fig. 1). The bouts were more often synchronised in enclosures than in stables and the rate of synchronised bouts decreased with increasing age of the foal.

3.2. Synchronised bouts and suckling bout duration

We found that suckling bout duration was affected by synchronised bouts ($F_{1,\ 5831} = 41.06$; $P < 0.01$), by the feeding status of the mother ($F_{2,\ 5831} = 37.23$; $P < 0.01$), the pregnancy status of the mother ($F_{1,\ 5831} = 24.42$; $P < 0.01$), the foal's age ($F_{1,\ 5831} = 120.64$; $P < 0.01$), the animal who terminated the suckling bout ($F_{1,\ 5831} = 328.70$; $P < 0.01$), the place where the suckling bout occurred ($F_{1,\ 5831} = 16.92$; $P < 0.01$), the number of other foals in the group ($F_{1,\ 5831} = 23.91$; $P < 0.01$) and the interaction between the species and the animal who terminated the suckling bout ($F_{2,\ 5831} = 61.88$; $P < 0.01$). Synchronised bouts lasted longer than non-synchronised bouts (Fig. 2). Also the suckling bout duration was longer in non-pregnant mothers than in pregnant ones, when the mother interrupted feeding due to nursing compared to when she was not feeding and when she was feeding continuously, when it occurred in the enclosure rather than in the stable, when terminated by the foal rather than by the mother and it increased with increasing numbers of foals in the group, as has been found in previous studies (Cameron et al., 2003; Pluháček et al., 2010a, 2014).

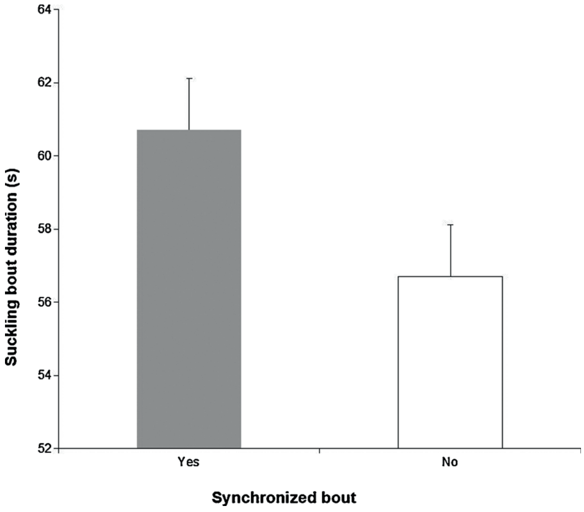

Fig. 2. The suckling bout duration for synchronised and non-synchronised suckling bouts in three captive zebra species (Least square means ± Standard errors).

In our next model we compared suckling bout duration between the "first foal" of the synchronised bout (=synchronised suckling bout by initial foal) and all other suckling bouts. We revealed that suckling bout duration was affected by synchronised suckling bout by initial foal ($F_{1,\ 5830} = 81.02$; $P < 0.01$), by the interaction of species and synchronised suckling bout by initial foal ($F_{2,\ 5830} = 4.26$; $P = 0.014$), by the interaction of animal which terminated the suckling bout and synchronised suckling bout by initial foal ($F_{1,\ 5830} = 10.32$; $P = 0.01$), by the feeding status of the mother ($F_{2,\ 5830} = 34.57$; $P < 0.01$), the pregnancy status of the mother ($F_{1,\ 5830} = 29.91$; $P < 0.01$), the foal's age ($F_{1,\ 5830} = 126.62$; $P < 0.01$), the animal who terminated the suckling bout ($F_{1,\ 5830} = 97.32$; $P < 0.01$), and by the interaction between the species and who terminated the suckling bout ($F_{2,\ 5830} = 63.97$; $P < 0.01$). In all three species the synchronised bouts of the foal that suckled first were longer than other bouts (Grevy's zebra $t = 6.41$; $P < 0.01$; mountain zebra $t = 5.00$; $P < 0.01$, plains zebra $t = 2.96$; $P < 0.01$). Whereas synchronised bout duration of the foal that started first did not differ interspecifically, the duration of other suckling bouts was shorter in Grevy's zebras than in plains zebras ($t = -2.91$; $P = 0.042$) and it tended to be shorter in Grevy's zebras than in mountain zebras ($t = -2.76$; $P = 0.064$). The suckling bout duration was longer in non-pregnant mothers than in pregnant ones, when the mother interrupted feeding due to nursing compared to when she was not feeding and when she was feeding continuously and when terminated by the foal rather than by the mother. The synchronised bout was longer when mountain zebra foals terminated the suckling bout than when Grevy's zebra foals ($t = -5.28$; $P < 0.01$) or plains zebra foals ($t = 4.47$; $P < 0.01$) terminated the suckling bout.

On the other hand, synchronised suckling bouts by second foal did not affect suckling bout duration. Thus, the "second foal" during synchronised suckling did not suckle for a longer time than the non-synchronised foals.

3.3. Termination of suckling bouts and synchronised bouts

The proportion of suckling bout termination by the mother was influenced by synchronised bouts ($\chi^2_1 = 4.92$; $P = 0.027$), by the foal's age ($\chi^2_1 = 7.74$; $P < 0.01$), by the feeding status of the mother before and during suckling ($\chi^2_2 = 7.21$; $P = 0.027$) and by species ($\chi^2_2 = 11.35$; $P < 0.01$) (Fig. 3). We found that the probability of terminating the suckling bout by the mother was lower when the suckling bout was synchronised rather than when it was not synchronised (Fig. 3). The probability of

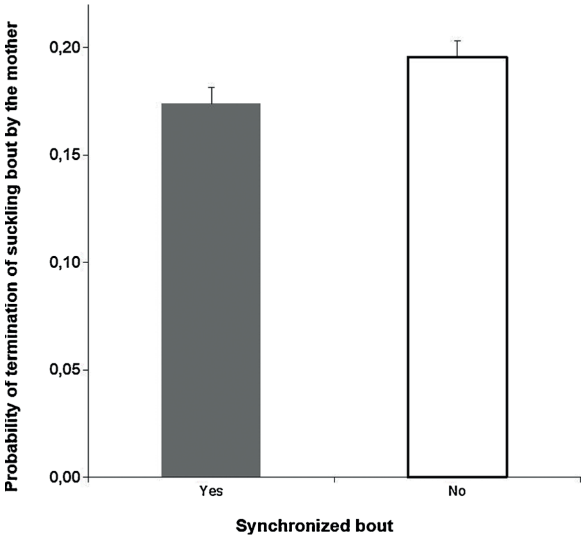

Fig. 3. The probability of termination by the mother for synchronised and non-synchronised suckling bouts in three captive zebra species (Least square means ± Standard errors).

suckling bout termination by the mother decreased with the age of the foal, it was lower when the mother was feeding than when she was not feeding or interrupted feeding due to nursing, and it was lower in Grevy's zebra, than in mountain zebra and plains zebra.

We found that the proportion of bouts terminated by the mother was influenced by synchronised suckling bouts by initial foal ($\chi^2_1 = 4.24$; $P = 0.039$), by the foal's age ($\chi^2_1 = 7.64$; $P < 0.01$), by feeding status of the mother before and during suckling ($\chi^2_2 = 7.14$; $P = 0.028$), and by the species ($\chi^2_2 = 11.36$; $P < 0.01$). Again, the synchronised bouts were less often terminated by the mother than the non-synchronised ones. Similarly as in the previous analysis, the probability of suckling bout termination by the mother decreased with increasing age of the foal, it was lower when the mother was feeding compared to when she was not feeding or interrupted feeding due to nursing, and was lower in Grevy's zebra, than in mountain zebra and plains zebra.

On the other hand synchronised suckling bouts by second foal did not affect the probability that the bout was terminated by the mother ($\chi^2_1 = 0.12$; $P = 0.73$).

4. Discussion

We found that almost one fifth (1036 out of 5890) of all suckling bouts were synchronised. When considering that average suckling bout duration is around one minute (Pluháček et al., 2010a; Pluháček et al., 2014) and the suckling rate is once per hour (Pluháček et al., 2010b, 2014), the rate of suckling synchronisation is quite a high. Since the foal is responsible for suckling initiation, it seems that when a foal observes suckling by another foal, it starts to engage in the same activity in line with the co-action theory of social facilitation (Zajonc, 1965). Thus, our findings suggest this type of social facilitation resulted in high rate of suckling by a second foal.

All but one study (Drews, 1991) that reported synchronisation of suckling behaviour were performed in polytocous species (Maletínská and Špinka, 2001; Wechsler and Brodmann, 1996). In these species, the synchronisation of suckling behaviour can be advantageous for lactating females to coordinate their daily activities (Wechsler and Brodmann, 1996) or to prevent allosuckling (Maletínská and Špinka, 2001). In monotocous species, such as equids, allosuckling is extremely rare (Cameron et al., 1999b; Olléová et al., 2012; Pluháček et al., 2011), making half-sibling competition over the available milk unlikely. Thus, in equids synchronised suckling can't be regarded as competitive behaviour among offspring.

In line with our predictions (1) and (2) and as well as the study of Drews (1991) on scimitar-horned oryx, our results revealed that synchronisation affected suckling bout duration and termination for the foal that started to suckle first, but not for the foal that started to suckle second. Therefore, we suggest that the longer suckling bouts, less often terminated by the mother of the "first foal of the synchronised pair", were due to the fact that either the mother or the foal saw the second pair beginning to suckle. These results could be well explained as an audience effect of social facilitation (Zajonc, 1965). This effect has been documented in many various species of ungulate (Conradt and Roper, 2000), birds (Collins and Sumpter, 2007; Keeling and Hurnik, 1996) and even in invertebrates (Kim, 2001).

Although, suckling bout duration might reflect the conflict over milk intake in some extreme cases such as allosuckling (Cameron et al., 1999b; Olléová et al., 2012; Pluháček et al., 2011), the termination of suckling bout by the mother represents the main behavioural parameter indicating a conflict (Cameron et al., 2003; Pluháček et al., 2010b, 2012). We found that mothers terminated synchronised bouts less often than non-synchronised ones. In addition, the suckling bouts terminated by the mother were shorter in duration than those terminated by foals (this study; Pluháček et al., 2012). Thus, the synchronised suckling diminished mother-offspring conflict for at least the first pair of the suckling dyad.

In addition, our results revealed that the occurrence of synchronised bouts (compared to non-synchronised ones) was affected by the species identity and by the number of foals in the group at the time of suckling. As several studies on various mammalian species have shown that interspecific differences in maternal behaviour are associated with variability of their social systems (Landete-Castillejos et al., 2000; Maestripieri, 1994; McGuire et al., 2011; Mcguire and Novak, 1984; Olléová et al., 2012; Pluháček et al., 2014, 2020), we suggest that our finding can be explained by the different social systems of the three zebra species. In plains and mountain zebra, the probability of synchronised bouts increased with increasing number of foals, whereas the opposite result was found in Grevy's zebra. Whereas plains and mountain zebra mares live together within one harem for most of their life (Klingel, 1967), lactating Grevy's zebra mares associate together after parturition and form nurseries of foals for the period of 3–6 months following the birth of foal (Ginsberg, 1988; Rowen, 1993; Rubenstein, 1989). We suggest three possible non-mutually exclusive explanations of this result. First, it may be that the Grevy's zebra foals tried to synchronize suckling mainly in smaller groups as in the wild the nurseries include mostly 2–3 mothers with foals (Becker and Ginsberg, 1990), whereas the increase in bout synchronisation of plains and mountain zebra may have simply reflected the increased number of foals within the band available to mimic. Second, it may be that the stronger social bonds in the harem-forming zebra species might produce more synchronisation between social partners. Conversely, contagion might be rarer between Grevy's females as they have only loose social bonds. Third it may be that in large Grevy's groups mothers tried to avoid synchronised bouts. However, this does not seem to be likely as previously we found that Grevy's zebra has lower mother's rejection and termination rates when compared with the two other species (Pluháček et al., 2012).

Further, we found no interspecific variation in the effect of synchronisation on the suckling bout duration by the first foal. This may indicate a strong effect of synchronisation on suckling bout duration in equids. Nevertheless, when considering only bouts terminated by foals (and not by the mother) then the suckling bout duration of mountain zebra lasted longer than that of the two other species. Thus, when not terminated by the mother, the effect of synchronisation was more pronounced in mountain zebra than in the two other species. This is a bit surprising in a species that forms the smallest groups where the synchronisation in behaviour of a foal is less likely (Joubert, 1974; Klingel, 1969, 1975; Penzhorn, 1984). On the other hand, we suggested previously that the longer suckling bout duration in mountain zebra compared with two other species might be an adaptation to high intra-group aggression in terms of supporting mother-young bonds (Pluháček et al., 2014). Thus, the mountain zebra foals (but not mothers) might be more motivated to prolong suckling when seeing another pair suckle to strengthen the bond with its mother compared to foals of more tolerant equid species. It could be also that the mother is less likely to be involved in aggression while several females are nursing, so the foal is taking advantage by suckling as long as it can before it is possibly interrupted by aggression within the group.

Our analysis revealed that the rate of synchronised bouts decreased with increasing age of the foal. Since foals are responsible for initiation of most suckling bouts (Pluháček et al., 2010a, b; Pluháček et al., 2012) it seems that they try to reduce mother-offspring conflict via synchronised suckling more in early lactation than at a later time. This suggestion is in line with the decrease of parent-offspring conflict in terms of lactation in captive zebras with increasing age of offspring (Pluháček et al., 2010a, 2012; Pluháček et al., 2014). Alternatively, the decline of synchronised suckling might simply reflect a decrease of suckling frequency with age. Although, the youngest foals do not spend on average more than 2 min of suckling per hour (Pluháček et al., 2010b, 2014), it is possible that less frequent visual/auditory/scent stimuli encouraging synchronised behaviour might result in fewer synchronised bouts in older foals.

We found that the bouts were more often synchronised in enclosures than in stables. This result might be explained by the fact that foals had a better view of the rest of the group in the larger outside space than in the smaller inside one. The enclosure might allow foals to synchronize not only suckling behaviour but also other activities such as play or resting behaviour. This finding stresses the importance of considering various environmental factors in research on basic mammalian behaviour such as suckling.

5. Conclusions

To our knowledge, except for the study of Drews (1991), this study remains the only one showing the effect of synchronisation on suckling bout duration, and represents the first one to report the effect of synchronisation on suckling bout termination in a monotocous mammalian species. As for some other synchronised behaviours, such as movement, vigilance, or resting (Couzin et al., 2002; Michelena et al., 2008; Öst and Tierala, 2011; Šárová et al., 2007; Sirot and Touzalin, 2009; Stoye et al., 2012), synchronised suckling resulting in longer suckling bouts and lower rate of mother's bout termination in monotocous mammals can be considered as advantageous. Longer suckling bouts may be beneficial for young regardless of the milk intake (Cassinello, 2001; Gomendio, 1990; Pluháček et al., 2014). Nevertheless, this advantage appears to be limited to the initial pair only. It does seem that social facilitation triggers the suckling behaviour of foals both by an audience effect (prolongation of suckling bout duration) as well as a co-action effect (occurrence of synchronisation). In addition, we found interspecific differences in pattern of suckling synchronisation among the three zebra species that might reflect the differences in social organisation. Last, the suckling bout synchronisation was most pronounced in early stages of lactation which coincides with the highest rate of parent-offspring conflict in captive zebra foals.

CRediT authorship contribution statement

Michaela Levá: Conceptualization, Data curation, Formal analysis, Investigation, Visualization, Writing - original draft. **Jan Pluháček:** Funding acquisition, Investigation, Methodology, Project administration, Supervision, Validation, Writing - review & editing, Investigation.

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2. Time spent suckling is affected by different social organisation in three zebra species.

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Time spent suckling is affected by different social organization in three zebra species

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Abstract

Suckling bout duration and frequency were used in the past as an indicator of milk intake. However, later studies found no significant relationship between suckling bout duration and frequency and milk or energy intake. On the other hand recent studies are in line with the suggestion that suckling bout duration and frequency may express intensity of maternal care. The three extant zebra species differ in their ecology and social system. Mountain *Equus zebra* and Grévy's zebra *E. grevyi* live in an arid environment, whereas plains zebras *E. quagga* are found in savannah. Mountain and plains zebra mares form stable herds associated with high aggression and low aggression, respectively. Female Grévy's zebras form loose associations with the lowest level of aggression. The aim of this study was to re-evaluate the suggestion that suckling bout duration and frequency are affected by social system. We observed suckling behaviour of 30 foals (16 plains zebras, 8 Grévy's zebras and 6 mountain zebras) at the Dvůr Králové Zoo, Czech Republic. We found that suckling bout duration was longest in mountain zebras, followed by plains and Grévy's zebras. Similar results were found for suckling frequency. These results coincide with the rate of aggression among mares; foals spent more time by suckling in species, where more aggression among adults occurred. Thus, the results of our study support the suggestion that suckling bout duration reflects social needs of the foal rather than milk intake requirements.

Introduction

In past studies on mammalian maternal investment, time spent suckling was often used as a predictor of the milk transferred to the infant (Duncan, Harvey & Wells, 1984; Berger, 1986; Green, 1986, 1990; Lee & Moss, 1986; Trillmich, 1990; Dalezsczyk, 2004). However, a meta-analysis of studies in mammals that have correlated measures of time spent suckling with milk intake estimates based on weight gain revealed a weak positive relationship and significant heterogeneity between studies (Cameron, 1998). In feral horses *Equus caballus* (Cameron *et al*., 1999), fallow deer *Dama dama* (Birgersson & Ekvall, 1994), domestic mice *Mus domesticus* (Mendl & Paul, 1989) domestic cats *Felis catus* (Mendl & Paul, 1989) and domestic cattle *Bos taurus* (Álvarez-Rodríguez *et al*., 2010), no significant relationship between suckling bout duration and/or suckling frequency and milk or energy intake was found. Suckling bout duration and frequency should not be used as an index of energy intake (Cameron *et al*., 1999); however, they can be used as an indication of conflict between the mare and foal over energy intake (Mendl & Paul, 1989; Byers & Bekoff, 1990; Cameron, Linklater & Stafford, 2003; Therrien *et al*., 2007).

The three extant zebra species differ in their behavioural ecology and social system. In the wild, mountain *E. zebra* and Grévy's zebras, *E. grevyi*, live in an arid environment, whereas plains zebras, *E. quagga*, inhabit more mesic savannah (Klingel, 1975; Estes, 1991). Mountain and plains zebra mares form stable herds involving a social hierarchy (Klingel, 1972; Penzhorn, 1979) associated with high aggression in the former and low aggression in the latter (Joubert, 1972*b*; Penzhorn, 1984; Lloyd & Rasa, 1989; Fischhoff *et al*., 2010). Aggression by adult mares towards unrelated foals has often been recorded in mountain zebra (Penzhorn, 1984; Lloyd & Rasa, 1989), but is very rare in plains zebra (Pluháček, Bartošová & Bartoš, 2010*c*). Female Grévy's zebras form only loose associations without any hierarchy (Klingel, 1974; Rubenstein, 1989; Sundaresan *et al*., 2007) and exhibit a lower level of aggression than the two other zebra species (Klingel, 1974; Penzhorn, 1984; Andersen, 1992; Pluháček, Bartoš & Čulík, 2006). Therefore, zebras form an optimal model for investigating the relationship between social organization and maternal behaviour.

Although an evolutionary approach has been suggested to understand the dynamics of parent–offspring relationships in mammals (Bateson, 1994), only few studies have compared the suckling behaviour in different species (e.g. Trillmich, 1990; Lavigueur & Barrette, 1992; Maestripieri, 1994*a*; McGuire, Vermeylen & Bemis, 2011). The only interspecific comparison of equid suckling behaviour was published from wild Grévy's and plains zebra (Becker & Ginsberg, 1990), comparing also data from the literature on feral horses (Tyler, 1972; Crowell-Davis, 1985). Becker & Ginsberg (1990) concluded that Grévy's zebra foals spent the least amount of time suckling and had the longest intervals between suckling bouts compared with other equids. They proposed that the shorter time spent by suckling found in Grévy's zebra compared with other equids would be an adaptation to arid environment (Becker & Ginsberg, 1990). Recently, we re-evaluate their suggestions using rejection and termination of suckling bouts (as indicators of conflict over energy intake) in three captive zebra species kept in the same facility (thus under same living conditions; Pluháček *et al.*, 2012).

On the other hand, we revealed higher incidence of allonursing in Grévy's zebra than in plains and mountain zebra, where allonursing was associated with adoption (Olléová, Pluháček & King, 2012). We suggested that higher tolerance towards non-filial offspring, including the occurrence of allosuckling in Grévy's zebras, could be affected by different social systems of zebra species as reported in several species of ungulates, rodents and primates (McGuire & Novak, 1984; Maestripieri, 1994*b*; Ekvall, 1998; Das, Redbo & Wiktorsson, 2000; Landete-Castillejos *et al.*, 2000; McGuire *et al.*, 2011).

Previous studies on suckling behaviour of various equid species (*E. caballus*, *E. hemoinus*, *E. quagga*, *E. zebra*) reported that suckling bout duration and frequency could be affected highly by the age and the sex of the foal, the animal terminating the bout, parity of the mare and mother's pregnancy (Joubert, 1972*b*; Tyler, 1972; Rogalski, 1973; Rashek, 1976; Duncan *et al.*, 1984; Crowell-Davis, 1985; Becker & Ginsberg, 1990; Smith-Funk & Crowell-Davis, 1992; Pluháček, Bartoš & Bartošová, 2010*a*; Bartošová *et al.*, 2011). Thus, we included these factors in our analyses, too.

Because suckling bout duration and frequency should not reflect energy intake, but the amount of maternal care in current offspring (Mendl & Paul, 1989; Cassinello, 2001; Therrien *et al.*, 2007; Pluháček *et al.*, 2010*a*; Bartošová *et al.*, 2011), we presume that they would be affected more by variability in social life of different species than by environmental adaptation. Therefore, we predicted that the time spent by suckling would increase with increasing intolerance towards foals in different zebra species, that is, foals of mountain zebras should spend the longest time by suckling, followed by foals of plains zebras and by foals of Grévy's zebras.

Materials and methods

Animals

We observed 30 foals (16 plains zebras, 8 Grévy's zebras and 6 mountain zebras) in five different herds (three of them being plains zebras) at the Dvůr Králové Zoo, Czech Republic (for details see Pluháček *et al.*, 2012; Table 1).

In the summer, all herds were in an enclosure (800–2800 m^2) for 24 h a day. From October to April, the zebras were stabled at night (stables were 62–194 m^2 per herd). Plains and Grévy's zebras were stabled in groups, whereas mountain zebra mares were stabled individually, but not separated from their foals. Therefore they were not observed in stables. Although a lactation study like this would be more realistic if it was done in the wild, it would be extremely difficult to carry out. Therefore even with potential constraints in interpretation, it represents a valuable piece of information.

Plains zebras were observed from January 1999 to January 2000, and from September 2001 to March 2002. All three species were observed from September 2008 to July 2010. Each observation session lasted for 180 min (started either from 08:00 or 14:00 h). For details of observation schedule see Pluháček *et al.* (2010*a*,*b*; 2012). In total, the three herds of plains zebras were observed for 549, 489 and 198 h; the herd of Grévy's zebras for 270 h; and the herd of mountain zebras for 120 h.

We used the same definitions of suckling bout, suckling attempt and interruption of suckling bouts as described in previous studies on equids (Becker & Ginsberg, 1990; Cameron *et al.*, 1999; for details about data collection, see Pluháček *et al.*, 2010*a*,*b*,*c*, 2012). Suckling bouts involving mares other than the mother (allosuckling) were excluded from analyses.

The frequency of suckling was counted as a number of successful suckling bouts per individual foal per one session (180 min). In total, we recorded 2193, 1705 and 842 successful suckling bouts and 455, 521 and 204 sessions per individual foals for respective species (plains zebras, Grévy's zebras and mountain zebras).

Statistics

All data were analysed using the SAS System version 9.2 (SAS Institute, Inc., Cary, NC, USA). Factors influencing the suckling bout duration and frequency were tested using a multivariate general linear mixed model (PROC MIXED, SAS Institute, Inc.). Fixed factors (independent variables) tested in each of the models were the foal's age and sex, the number of dominant mares (at the date of suckling bout), the herd nested within the season (1999/2000, 2001/2002, 2008/2010), the mother's age, the mother's parity, the number of other suckling foals within the herd, the number of other animals in the herd, the number of previous births of the mother, the number of offspring successfully reared by the mother, the place where the suckling bout occurred (stable, yard or enclosure; in analyses of suckling bout duration only), and the feeding state of the mother ('yes', 'no', 'interrupted due to nursing'; in analyses of suckling bout duration only), and their first-order interaction terms.

In all models, repeated measures on the same individuals across the period of observation were handled with the individual foal entering the model as a *subject* in the *repeated* statement. The within-group means were appropriately adjusted for the other effects in the model (least-squares

Table 1 Detailed individual data of observed foals of three zebra species

Foal	Mother	Species	Sex	Herd identity and season	Age of foal at start of observation (in days)	Age of foal at end of observation (in days)
Pergy	Piki	*Equus quagga*	F	1/1999	36	113
Pelopones	Pinta	*E. quagga*	M	1/1999	0	330
Paris	Palmyra	*E. quagga*	M	1/2001	96	278
Ptolemaios	Piki	*E. quagga*	M	1/2001	94	276
Paula	Palmyra	*E. quagga*	F	1/2008	4	432
Rubi	Karma	*E. quagga*	F	1/2008	2	261
Irwin	Irkasa	*E. quagga*	M	1/2008	4	298
Linda	Karolína	*E. quagga*	F	1/2008	4	173
Masud	Meri	*E. quagga*	M	2/1999	3	143
Delos	Duky	*E. quagga*	M	2/1999	0	84
Akin	Alžběta	*E. quagga*	M	2/2008	100	394
Padme	Penta	*E. quagga*	F	2/2008	26	320
Kid	Kity	*E. quagga*	M	3/1999	1	245
Beata	Boma	*E. quagga*	F	3/1999	4	75
Accra	Angelika	*E. quagga*	F	3/2001	3	101
Kikwit	Katrin	*E. quagga*	M	3/2001	3	101
Ajka	Arica	*E. grevyi*	F	4/2008	3	333
Alf	Ambra	*E. grevyi*	M	4/2008	5	377
Belinda	Tabia	*E. grevyi*	F	4/2008	8	394
Guru	Gizela	*E. grevyi*	M	4/2008	1	352
Hedvika	Gobi	*E. grevyi*	F	4/2008	9	395
Kevin	Šárka2	*E. grevyi*	M	4/2008	5	174
Lukrinda	Šelda	*E. grevyi*	F	4/2008	5	369
Naomi	Nora	*E. grevyi*	F	4/2008	2	374
Belisa	Bonita	*E. zebra*	F	5/2008	24	396
Brenda	Beata	*E. zebra*	F	5/2008	10	382
Lenka	Lada	*E. zebra*	F	5/2008	25	397
Lola	Linda	*E. zebra*	F	5/2008	30	366
Mája	Manka	*E. zebra*	F	5/2008	0	358
Hasan	Halina	*E. zebra*	M	5/2008	4	362

means statement). The differences between the means were tested by *t*-test; with multiple comparisons we used the Tukey–Kramer adjustment.

Results

Suckling bout duration

Average suckling bout duration lasted for 57.32 ± 25.02 s (n = 1689 bouts) in Grévy's zebra, 60.24 ± 19.64 s (n = 2012 bouts) in plains zebra and 71.95 ± 27.64 s (n = 835 bouts) in mountain zebras. The longest suckling bout lasted for 4 min and 16 s in Grévy's zebras, 4 min and 35 s in plains zebras, and 3 min and 14 s in mountain zebras.

The duration of suckling bouts decreased with increasing age of the foal [$F = 173.00$; degrees of freedom (d.f.) = 1, 4497; $P < 0.001$]. Duration was affected by the animal that terminated the bout ($F = 178.19$; d.f. = 2, 4497; $P < 0.001$), by the interaction between species and the animal that terminated the bout ($F = 22.09$; d.f. = 4, 4497; $P < 0.001$), and by the feeding status of the mare at the beginning of the suckling bout ($F = 31.46$; d.f. = 2, 4497; $P < 0.001$).

In all three zebra species, suckling bouts terminated by the foal were longer than those terminated by the mare (plains zebras: $t = 7.97$, d.f. = 4497, $P < 0.001$; Grévy's zebras: $t = 6.88$, d.f. = 4497, $P < 0.001$; mountain zebras: $t = 14.83$, d.f. = 4497, $P < 0.001$) or by a herdmate (plains zebras: $t = 5.81$, d.f. = 4497, $P < 0.001$; Grévy's zebras: $t = 2.59$, d.f. = 4497, $P = 0.01$; mountain zebras: $t = 6.28$, d.f. = 4497, $P < 0.001$; Fig. 1). The suckling bouts were shorter when terminated by a herdmate than when terminated by the mare in plains zebras only ($t = 3.49$, d.f. = 4497, $P = 0.015$). When the mother interrupted feeding because of nursing, then the suckling bouts duration lasted longer than when the mother did not feed ($t = 3.65$, d.f. = 4497, $P < 0.001$) or when she was feeding during the whole bout ($t = 7.86$, d.f. = 4497, $P < 0.001$). The suckling bout duration was longer when she was not feeding than when she was feeding while nursing ($t = 6.28$, d.f. = 4497, $P < 0.001$). No other factor was significant.

For the next step, we ran three separate analyses for suckling bout duration in bouts terminated by the foal, by the mare and by a herdmate. When terminated by a herdmate, the suckling bout duration did not differ among species [$F = 0.60$; d.f. = 2, 53; not significant (NS)]; when terminated by the mare, suckling bout duration did differ among species (F =

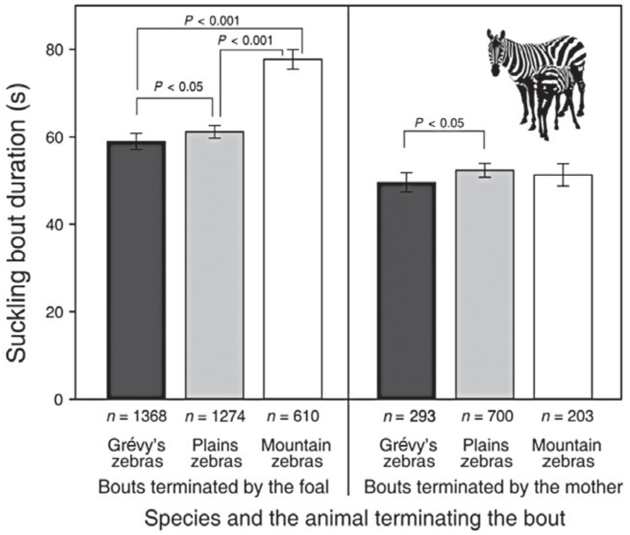

Figure 1 The suckling bout duration in three zebra species according to the animal terminating the bout and the identity of species (mean ± standard error). Only significant differences among species are shown.

3.26; d.f. = 2, 1162; $P = 0.033$): suckling bout duration was shorter in Grévy's zebras than in plains zebras ($t = 2.65$; d.f. = 1162; $P < 0.011$; Fig. 1). The suckling bout duration terminated by a mountain zebra mare did not differ from that of the other species (Fig. 1). When terminated by a foal, again the suckling bout duration differed among species ($F = 19.04$; d.f. = 2, 3239; $P < 0.001$). The suckling bout duration was longer in mountain zebras than in plains ($t = 4.87$, d.f. = 3239, $P < 0.001$) or Grévy's zebras ($t = 6.03$, d.f. = 3239, $P < 0.001$), and it was longer in plains zebras than in Grévy's zebras ($t = 1.95$, d.f. = 3239, $P = 0.049$; Fig. 1).

Suckling bout frequency and total time spent by suckling

Average suckling frequency per 180 min was 3.29 ± 2.14 (n = 521 individual sessions), 4.68 ± 2.42 ($n = 455$) and 3.92 ± 2.25 ($n = 204$) in Grévy's, plains and mountain zebras, respectively. The maximum suckling bout frequency per 180 min (one observation session) in three species was 17 times in Grévy's zebras, 22 times in plains zebras and 13 times in mountain zebras. The lowest suckling bout frequency was once per 180 min (all three species).

Suckling bout frequency has been affected by the age of the foal ($F = 582.83$; d.f. = 1, 1147; $P < 0.001$), by the species ($F = 7.99$; d.f. = 2, 1147; $P < 0.001$) and by the interaction between the age of the foal and the species ($F = 12.51$; d.f. = 1, 1147; $P < 0.001$; Fig. 2). The highest suckling bout frequency has been observed in plains zebras followed by that of mountain zebras ($t = 4.80$, d.f. = 1147, $P < 0.001$), and the lowest suckling frequency has been recorded in Grévy's zebras ($t = 4.25$, d.f. = 1147, $P < 0.001$). Similarly, the total time spent suckling during one observation period was affected by the age of the foal ($F = 673.06$; d.f. = 1, 1147; $P < 0.001$), by the species ($F = 7.41$; d.f. = 1, 1147; $P < 0.001$) and by the interaction between the age of the foal and the species ($F = 10.63$; d.f. = 1, 1147; $P < 0.001$). The time spent by suckling during observation session recorded in Grévy's zebras (202.04 ± 20.19 s per session) was shorter than that found in mountain zebras (292.59 ± 23.93 s per session; $t = 2.89$, d.f. = 1147, $P = 0.011$), whereas we did not find any difference between plains zebras (239.48 ± 15.93 s per session) and two other species (NS; Fig. 3).

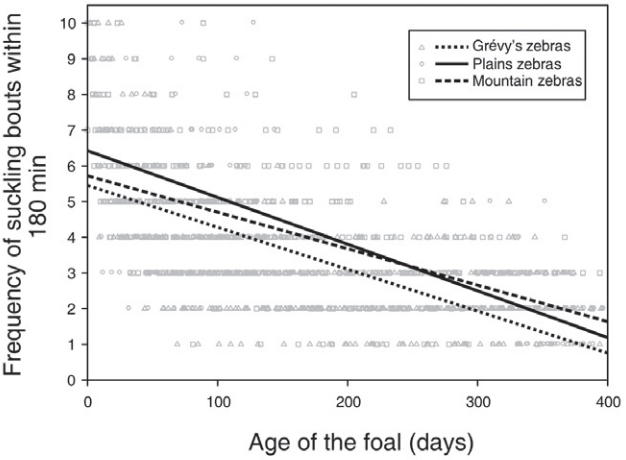

Figure 2 The frequency of suckling bouts within the 180-min observation session according to the age of foal and the species.

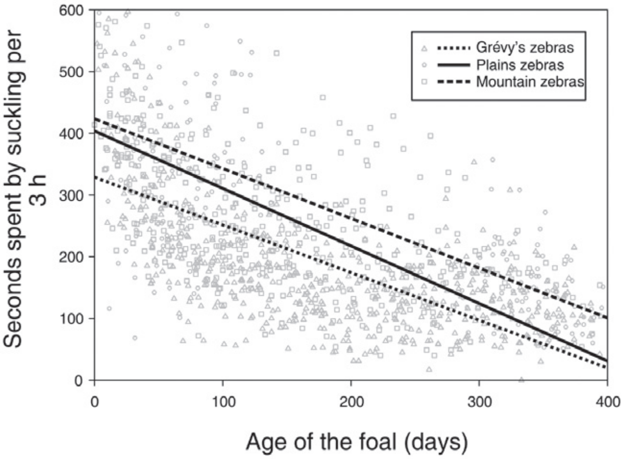

Figure 3 The total time spent by suckling within the 180-min observation session according to the species.

Rate of agonistic interactions

In total we recorded 2312 agonistic interactions among adult mares. The rate of agonistic interactions per individual during 1 h of observation was highest in mountain zebras (0.90), lower in plains zebras (0.52) and lowest in Grévy's zebras (0.09; $\chi^2 = 25.81$, d.f. = 2, $P < 0.001$).

Discussion

We found that suckling bout duration was the longest and most frequent in mountain zebra, followed by plains and Grévy's zebra. Thus, suckling bout duration in captive animals does not necessarily reflect evolutionary adaptation to an arid environment. Although suckling bout duration and frequency is not a good indicator of milk transfer (Cameron, 1998; Cameron *et al*., 1999), it can be useful to assess the amount of maternal care in current offspring (Mendl & Paul, 1989; Cassinello, 2001; Therrien *et al*., 2007; Pluháček *et al*., 2010*a*) and specifically the needs of the offspring (e.g. suckling frequency in Therrien *et al*., 2007). Our results suggested that suckling bout duration increased with intraspecific aggression rate among adult females of the species (i.e. longest duration recorded in mountain zebras, followed by plains zebras and Grévy's zebras). A similar effect of relationships among adults, including aggression among female adults on maternal style, was recorded in interspecific comparisons of several macaque species (Kaufman & Rosenblum, 1969; Thierry, 1985; Maestripieri, 1994*a*,*b*). This has been given as a possible explanation for high-suckling frequency in studies on white-tailed deer *Odocoileus virginianus* and fallow deer (Lavigueur & Barrette, 1992; Therrien *et al*., 2007). In primates suckling duration is correlated with stress reduction (Gomendio, 1990; Clutton-Brock, 1991; Redondo, Gomendio & Medina, 1992), and in cattle with socialization with the dam (Das *et al*., 2000). Therefore, suckling bout duration and the time spent suckling can reflect the social needs of the foal, whereas termination and rejection seems to be affected by ecological adaptation. Because our results came from captive animals living in limited space, the high aggression rate among mares could strengthen the social demands of the foal to the mother, in mountain zebras in particular. The artificial setting may also have affected the results likely by two factors: smaller space than in the wild and high-quality diet of predictable delivery.

Our results dealing with suckling bout duration and frequency are a little different from those of Becker & Ginsberg (1990). In both studies the lowest suckling frequency and time spent suckling was observed in Grévy's zebras. However, contrasting with the results of Becker & Ginsberg (1990) we recorded longer suckling bout duration in plains than in Grévy's zebras. In our earlier study on captive plains zebras, we found that suckling bout duration was highly affected by the animal terminating the bout and by the pregnancy status of the nursing mare (Pluháček *et al*., 2010*a*); in this study we excluded pregnant mares and did separate analyses depending on the animal terminating the bout. These factors could have affected the results of Becker & Ginsberg (1990). Nevertheless, we cannot omit the effect of captivity as an explanation for the difference in suckling bout duration between our and their studies.

This study including all three zebra species confirmed our previous results on plains zebras (Pluháček *et al*., 2010*a*) showing the importance of the animal terminating the bout on the duration of the bout. In all three species the suckling bout duration was shorter when terminated by the mother than when terminated by the foal. Similar results were observed in other ungulates as, for example, red deer *Cervus elaphus* (Bartošová, Ceacero & Bartoš, 2012) or babirusa *Babyrousa babyrussa* (MacLaughlin *et al*., 2000). Because we did not find any substantial interspecific differences among suckling bout duration terminated by mother, we suppose that the level of parent–offspring conflict (Trivers, 1974) did not differ highly among different zebra species. On the other hand the interspecific differences were most pronounced in bouts terminated by the foal. It shows that the foals of different species differed in their intention for how long to suckle. As suckling bout duration should not reflect milk intake (Cameron, 1998; Cameron *et al*., 1999), and because the foals in our study suckled longer when not terminated by the mother in species with higher rate of agonistic interactions among mares, our results support the suggestion that suckling bout duration reflect psychological needs of the young.

In line with most studies on ungulates (Gauthier & Barrette, 1985; Byers & Moodie, 1990; Green, 1990; Lent, 1991; Birgersson & Ekvall, 1994; Alley, Fordham & Minot, 1995; Špinka & Algers, 1995; Das *et al*., 2000; Dalezsczyk, 2004), we found that suckling bout duration and frequency decreased with increasing age of the foal in all three observed zebra species. However, in several ungulate species (cattle, impala *Aepyceros melampus*, Sumatran rhinoceros *Dicerorhinus sumatrensis*), suckling bout duration is not affected by the age of the young (Lewandrowski & Hurnik, 1983; Mooring & Rubin, 1991; Plair, Reinhart & Roth, 2012) or even increased with an increasing age of the young (eland *Taurotragus oryx*; Underwood, 1979; common hippopotamus *Hippopotamus amphibius*; Pluháček & Bartošová, 2011). Therefore, we suggest that suckling bout duration seems to be better indicator of offspring needs than suckling frequency.

This study offers the first detailed report of suckling bout duration and frequency in mountain zebra. Mountain zebras in the present study had the longest suckling bout duration when considering bouts terminated by foal of the three zebra species. This coincides with reports from the wild suggesting that 'the total suckling time usually varies from 90 s to 2 min' (Joubert, 1972*a*,*b*; Penzhorn, 1984), which are among the highest values reported for equids (Waring, 2003). On the other hand, we did not record any interruption 10 s before the end of the bout as reported from the wild (Joubert, 1972*a*,*b*; Penzhorn, 1984). The higher suckling frequency of mountain zebra recorded in our study compared with other studies on the same species (Joubert, 1972*b*; Penzhorn, 1984) could be explained by captive conditions including water availability.

In conclusion, our results showing that suckling bout duration seems to reflect aggression rate among mares of the different zebra species are in line with the hypothesis that suckling bout duration indicates the social needs of the foal rather than milk intake requirements.

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3. Effect of ecological adaptation on suckling behaviour in three zebra species

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Effect of ecological adaptation on suckling behaviour in three zebra species

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Abstract

The three existing zebra species differ in their ecology: in the wild, mountain (*Equus zebra*) and Grevy's zebra (*Equus grevyi*) live in an arid environment while plains zebra (*Equus quagga*) inhabit savannah. Interspecific differences in maternal care in terms of suckling bout duration and frequency are thought to be based on the ecological adaptations of equid species. However, other studies showed that suckling bout duration and frequency cannot reflect maternal investment. The aim of this study was to re-evaluate the suggestion of previous studies that suckling behaviour is influenced by environmental adaptations in equids using rejection and termination of suckling bouts in three captive zebra species kept in the same facility. Suckling behaviour of all three zebra species was observed over a period of 31 months at the Dvůr Králové Zoo, Czech Republic. We found that Grevy's and mountain zebra showed a lower rate of rejection and termination of suckling bouts by the mother than plains zebra. Therefore, mothers of species that evolved in a more arid habitat were more tolerant towards their offspring than those of species that evolved in a mesic habitat. Thus, our results confirmed that parent–offspring conflict in terms of suckling bout termination and rejection seems to be affected by ecological adaptation.

Keywords

Equus, suckling behaviour, zebra, parent–offspring conflict, maternal care.

1. Introduction

"The key to sociobiology of mammals is milk" (Wilson, 1975). Lactation is a far more demanding form of maternal investment than gestation, oestrus

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behaviour or ovulation (Sadleir, 1984). Lactation affects social behaviour of herds as it is a key determinant of leadership, and plays an important role in individual as well as herd movements in wild plains zebra (*Equus quagga*: Fischhoff et al., 2007), Grevy's zebra (*Equus grevyi*: Sundaresan et al., 2007b), feral horses (*Equus caballus*: Rubenstein, 1993), and other ungulates (e.g., American bison *Bison bison*: Green, 1990).

The three extant zebra species differ in their behavioural ecology and social system. In the wild, mountain (*Equus zebra*) and Grevy's zebra live in an arid environment, while plains zebra inhabit more mesic savannah (Klingel, 1975; Estes, 1991). Mountain and plains zebra mares form stable herds involving a social hierarchy (Klingel, 1972; Penzhorn, 1979) associated with high aggression in the former and low aggression in the latter (Joubert, 1972b; Penzhorn, 1984a; Lloyd & Rasa, 1989; Fischhoff et al., 2010). Aggression by adult mares towards unrelated foals has often been recorded in mountain zebra (Penzhorn, 1984a; Lloyd & Rasa, 1989), but is very rare in plains zebra (Pluháček et al., 2010c). Grevy's zebra females form only loose associations without any visible hierarchy (Klingel, 1974; Rubenstein, 1989; Sundaresan et al., 2007a), and exhibit a lower level of aggression than the two other zebra species (Klingel, 1974; Penzhorn, 1984a; Andersen, 1992).

All equid species are categorized as followers (Ralls et al., 1987; Estes, 1991). In some aspects mare-infant behaviour is affected by the social organization of zebras. Whereas Grevy's zebra form crèches or leave foals alone while the mother travels to water, mountain and plains zebra foals remain within the natal herd (Klingel, 1969, 1974; Joubert, 1972a; Penzhorn, 1984a; Ginsberg, 1989).

Although an evolutionary approach has been suggested to understand the dynamics of parent–offspring relationships in mammals (Bateson, 1994), only a few studies have compared the suckling behaviour of several species (e.g., sea lions Otaridae: Trillmich, 1990; fallow deer *Dama dama* and white-tailed deer *Odocoileus virginianus*: Gauthier & Barrette, 1985; rhesus macaque *Macaca mulatta*, pigtail macaque *M. nemestrina* and stumptail macaque *M. arctoides*: Maestripieri, 1994a). These studies showed that habitat, e.g., latitude in otarids (Trillmich, 1990), or feeding conditions where the species evolved (Maestripieri, 1994a) affects maternal investment. In several mammals, differences in mother-infant relationships are affected by social organization, for example nipple attachment and switching in voles

(McGuire et al., 2011) or occurrence of allosuckling in different deer populations (Ekvall, 1998; Landete-Castillejos et al., 2000). The three zebra species inhabit different environments and vary in social organization, making them good study organisms for investigating relationships between social organization and maternal behaviour. The only interspecific comparison of equid suckling behaviour was from wild Grevy's and plains zebra (Becker & Ginsberg, 1990), including also data from the literature on feral horses (Tyler, 1972; Crowell-Davis, 1985). Becker & Ginsberg (1990) found that Grevy's zebra foals spent the least amount of time suckling and had the longest intervals between suckling bouts compared to other equids. Thus, Grevy's zebra foals reduce the amount of time in which they are dependent on their mothers for their nutrition. Therefore, they proposed that the accelerated foal development in Grevy's zebra compared to other equids would be an adaptation to an arid environment (Becker & Ginsberg, 1990).

However, ten years later a meta-analysis of studies in mammals correlating measures of time spent suckling with milk intake estimates based on weight gain revealed a weak positive relationship and significant heterogeneity between studies (Cameron, 1998). Moreover, in feral horses (Cameron et al., 1999), fallow deer (*Dama dama*: Birgersson & Ekvall, 1994), domestic mice (*Mus domesticus*: Mendl & Paul, 1989) and domestic cats (*Felis cattus*: Mendl & Paul, 1989), no significant relationship between suckling bout duration and/or suckling frequency and milk or energy intake was found. In one of the very few studies comparing frequency of suckling bouts with milk production measured directly by milking the mother, both variables decreased jointly (i.e., correlated positively) as lactation went on (Landete-Castillejos et al., 2000). On the other hand, the termination and rejection of suckling should be used as a more reliable behavioural measure of parent–offspring conflict over resources (Trivers, 1974; Green et al., 1993; Birgersson & Ekvall, 1994). A high rate of suckling attempts rejected by the mother and suckling bouts terminated by the mother, rather than by the foal, should indicate high levels of conflict over resources (Green et al., 1993; Cameron et al., 2000, 2003; Cameron & Linklater, 2000). Nevertheless, Becker & Ginsberg (1990) did not include rejection and termination of suckling bouts in their analyses.

Reports of suckling behaviour in mountain and Grevy's zebra are very rare, with no detailed information about the number of animals observed

(Joubert, 1972b; Penzhorn, 1984b; Rowen, 1993). Thus, basic biological information concerning the suckling behaviour of these equid species is needed (Fisher et al., 2002).

The differences in behavioural characteristics of mother-infant behaviour including suckling behaviour have been reported either between species (Maestripieri, 1994a, b) or between breeds of domestic animals (Carson & Wood-Gush, 1983; Dwyer & Lawrence, 2000a, b). If these differences are of genetic origin they should be detectable and persist in captivity (Maestripieri, 1994a; McGuire et al., 2011), as the underlying factor of suckling observations is milk transfer. Food availability can greatly influence milk production and composition in wild ungulates such as red deer (*Cervus elaphus* Landete-Castillejos et al., 2003a). However, other studies of red deer showed that genetic differences even at the level of subspecies can produce differences in milk production and composition, even when the two subspecies are housed under the same conditions and diet (Landete-Castillejos et al., 2003b). Therefore, the main aim of this study is to re-evaluate the suggestions made by Becker & Ginsberg (1990) that suckling behaviour reflects adaptation to the habitat quality where the species evolved, tested through rejection and termination of suckling bouts in three captive zebra species kept in the same facility (thus under the same living conditions).

2. Methods

2.1. Animals

We observed 43 foals (29 plains zebra, 8 Grevy’s zebra and 6 mountain zebra) in five different herds (three of which were plains zebra) at the Dvůr Králové Zoo, Czech Republic (see Table 1). The herd sizes ranged from two to 14 breeding mares involving 1–8 mother-foal dyads, aged from 4 to 27 years. All but six of the observed adult mares were multiparous. Since pregnancy of the mother can affect suckling behaviour in equids (Pluháček et al., 2010a; Bartošová, et al., 2011) and mammals in general (Green et al., 1993; Bateson, 1994), we excluded foals of pregnant mares (13 plains zebra) from all the analyses.

In the summer all herds were in an enclosure (800 to 2800 m^2) 24 h a day. From October to April the zebras were stabled at night (stables were 62 to 194 m^2 per herd). Plains and Grevy’s zebras were stabled in groups, mountain zebra mares were stabled individually and, therefore, they were

Table 1.
Detailed individual data of observed foals of three zebra species.

Foal	Mother	Species	Sex	Herd identity and season	Age of foal at start of observation (in days)	Age of foal at end of observation (in days)
Pergy	Piki	*E. quagga*	F	1/1999	36	113
Pelopones	Pinta	*E. quagga*	M	1/1999	0	330
Paris	Palmyra	*E. quagga*	M	1/2001	96	278
Ptolemaios	Piki	*E. quagga*	M	1/2001	94	276
Paula	Palmyra	*E. quagga*	F	1/2008	4	432
Rubi	Karma	*E. quagga*	F	1/2008	2	261
Irwin	Irkasa	*E. quagga*	M	1/2008	4	298
Linda	Karolína	*E. quagga*	F	1/2008	4	173
Masud	Meri	*E. quagga*	M	2/1999	3	143
Delos	Duky	*E. quagga*	M	2/1999	0	84
Akin	Alžběta	*E. quagga*	M	2/2008	100	394
Padme	Penta	*E. quagga*	F	2/2008	26	320
Kid	Kity	*E. quagga*	M	3/1999	1	245
Beata	Boma	*E. quagga*	F	3/1999	4	75
Accra	Angelika	*E. quagga*	F	3/2001	3	101
Kikwit	Katrin	*E. quagga*	M	3/2001	3	101
Ajka	Arica	*E. grevyi*	F	4/2008	3	333
Alf	Ambra	*E. grevyi*	M	4/2008	5	377
Belinda	Tabia	*E. grevyi*	F	4/2008	8	394
Guru	Gizela	*E. grevyi*	M	4/2008	1	352
Hedvika	Gobi	*E. grevyi*	F	4/2008	9	395
Kevin	Šárka2	*E. grevyi*	M	4/2008	5	174
Lukrinda	Šelda	*E. grevyi*	F	4/2008	5	369
Naomi	Nora	*E. grevyi*	F	4/2008	2	374
Belisa	Bonita	*E. zebra*	F	5/2008	24	396
Brenda	Beata	*E. zebra*	F	5/2008	10	382
Lenka	Lada	*E. zebra*	F	5/2008	25	397
Lola	Linda	*E. zebra*	F	5/2008	30	381
Mája	Manka	*E. zebra*	F	5/2008	0	358
Hasan	Halina	*E. zebra*	M	5/2008	4	362

not observed in stables. There was almost no vegetation present in any of the enclosures. Hay or grass (during summer) and water were provided ad libitum. Food also included pellets, carrots and vitamins given fresh daily, usually in the morning. Individuals were identified by their unique striping pattern. Plains zebra were observed from January 1999 to January 2000 and from September 2001 to March 2002. All three species were observed from September 2008 to July 2010. We performed the observations in four different sessions each week. Each session lasted 180 min, either from 08:00 h to 11:00 h or from 14:00 h to 17:00 h on Saturday or Sunday. This timing reflected peaks of suckling activity found in wild and feral equid populations (Joubert, 1972a). We observed only one herd during each session (i.e., on Saturday we observed Herd 1 in the morning, Herd 2 in the afternoon; on Sunday we observed Herd 3 in the morning, and in the afternoon Herd 1 again; the next Saturday we began with Herd 2, etc.). In total, we carried out 1626 hours of observation (542 sessions over 299 days). The respective herds were observed for 552 (Herd 1 of plains zebra), 486 (Herd 2 of plains zebra), 198 (Herd 3 of plains zebra), 270 (Grevy's zebra) and 120 (mountain zebra) hours.

In each observation session we collected all data concerning any suckling event (ad libitum sampling method; Altmann, 1974) continuously using a tape recorder. We used the same definitions of suckling bout, suckling attempt and interruption of suckling bouts as described in previous studies on equids (Becker & Ginsberg, 1990; Cameron et al., 1999; for details see also Pluháček et al., 2010a, b, c). The suckling bout was regarded as successful when it lasted longer than five seconds and was not interrupted for longer than 60 s. If the interruption of a suckling bout was longer than 60 s, it was considered two suckling bouts. Suckling lasting less than 5 s, and cases in which foals approached their mother and she walked away or did not allow the foals to make contact with the teats using her legs were defined as suckling attempts rejected by the mare. We recorded the following data for each suckling bout or suckling attempt that was observed: the foal's and mother's identity; the animal that initiated (foal or mother), terminated or interrupted (foal, mother, other herdmate or disturbance by people) a suckling bout; the place (stable, yard (small outside paddock), enclosure).

All other data concerning the animals (i.e., date of birth of the foals and parents, number of previous foals of the mother, etc.) were obtained from curators of the Dvůr Králové Zoo. Suckling bouts and attempts involving mares other than the mother were excluded from analyses.

2.2. *Statistics*

All data were analyzed using the SAS System, Version 9.2. To assess the impact of tested factors on suckling bouts and suckling attempts terminated by the mother, we applied an analysis of categorical repeated measurements based on the generalized estimating equation approach (Liang & Zeger, 1986) using the logistic regression model (GENMOD procedure in SAS, distribution = binomial, link function = logit). We tested the probability that (i) the suckling bout was successful (i.e., not rejected by the mother within 5 s) and (ii) the mother terminated the suckling bout. Therefore, the dependent variables entered the particular analysis as (i) rejection of a suckling attempt by the mother within five seconds (yes/no) and (ii) termination of a suckling bout (mother/foal). Predictors (independent variables) tested in each of the two models were the foal's age and sex, the number of dominant mares (at the date of suckling bout), the herd nested within the season (1999/2000, 2001/2002 and 2008/2010), the mother's age, mother's parity (primiparous, multiparous), the number of other animals in the herd (from 1 to 25), the number of previous births of the mother (from 0 to 15), the number of offspring successfully reared by the mother (from 0 to 12), the place where the suckling bout occurred (stable, yard, or enclosure), and the feeding state of the mother ('yes', 'no', 'interrupted due to nursing'), and second way interactions between main predictors. In each analysis the number of factors examined was below what degrees of freedom allows for an appropriate analysis.

In all models repeated measures on the same individuals across the period of observation were handled with the individual foal 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 which were not significant.

3. Results

In total, we recorded 4713 successful suckling bouts and 2779 unsuccessful suckling attempts rejected by the mare. For respective species (plains zebra, Grevy's zebra and mountain zebra) we recorded 2141, 1729 and 843 successful suckling bouts, and 1659, 825 and 295 unsuccessful suckling attempts rejected by the mare.

3.1. Rejection of suckling attempts

The logistic regression model showed that the interaction between age of the foal and species ($\chi^2 = 7.47$; df $= 2$; $p = 0.024$; Figure 1) was related

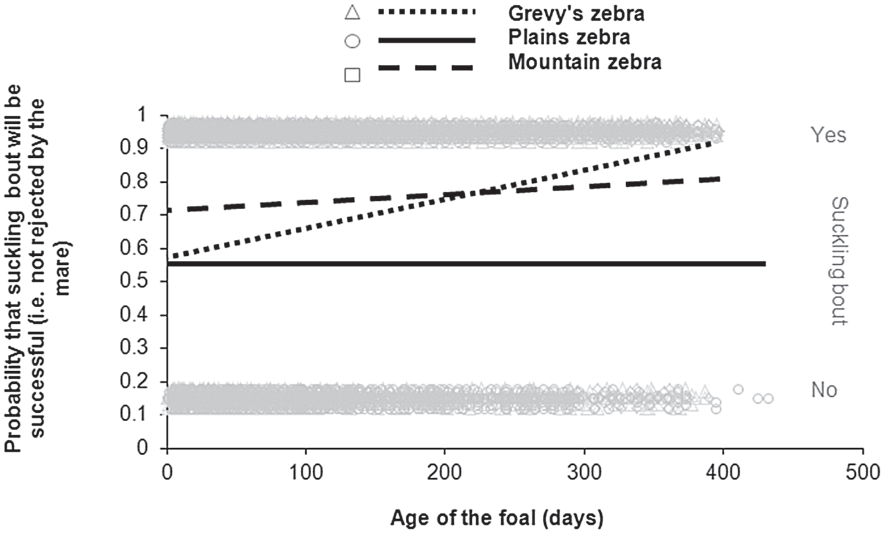

Figure 1. The probability that suckling bout will be successful (i.e., not rejected by the mare) in three zebra species according to the age of foal and the species (logistic regression, PROC GENMOD, SAS 9.2). Gray symbols reflect observed numbers of successful suckling bouts (upper row) and unsuccessful attempts rejected by the mare (lower row). The figure is based on 2554 solicitations observed in 8 foals of Grevy's zebra, 3800 solicitations in 16 foals of plains zebra and 1138 solicitations in 6 foals in mountain zebra.

to the probability of rejection. Plains zebra mares refused more solicitations by the foal (44%, $N = 3800$) than Grevy's zebra (32%; $N = 2554$; $\chi^2 = 15.49$; df $= 1$; $p < 0.001$) or mountain zebra (26%, $N = 1138$; $\chi^2 = 30.42$; df $= 1$; $p < 0.0001$). The probability of rejection did not change in plains or mountain zebra, but it decreased with increasing age of the foal in Grevy's zebra ($Z = 2.99$; $p = 0.003$). The last factor affecting the probability of rejection was feeding status of the mother ($\chi^2 = 11.75$, df $= 1$; $p < 0.001$). When the mare was feeding as the foal began to suckle there was a higher probability of refusing the suckling attempt (44%, $N = 2607$) than when she was not feeding (33%, $N = 4885$). No other factor was significant.

3.2. Suckling bout termination

The probability of suckling bouts being terminated by the mother was affected by the foal's age ($\chi^2 = 11.88$; df $= 1$; $p < 0.001$), the interaction between the foal's age and species ($\chi^2 = 6.93$; df $= 2$; $p = 0.031$; Figure 2), and the feeding status of the mother at the start of the suckling bout

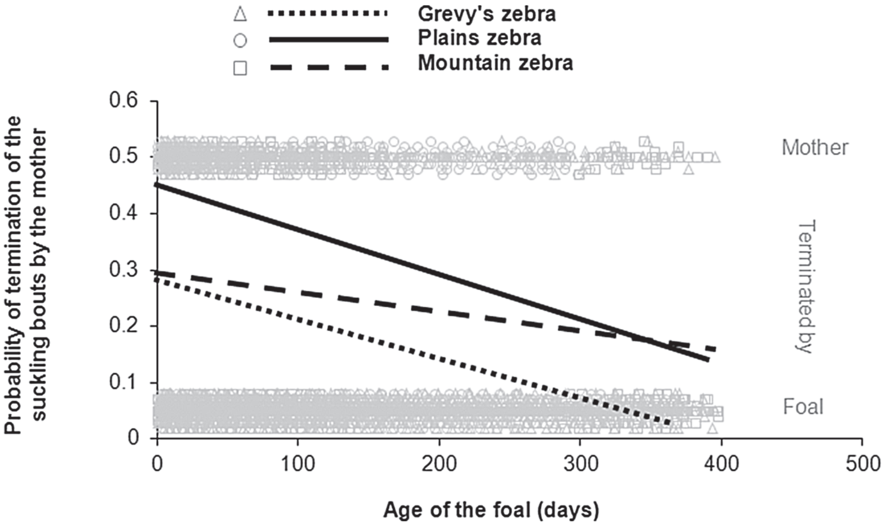

Figure 2. The probability of suckling bouts terminated by the mother and not by the foal in three zebra species according to the age of foal and the species (logistic regression, PROC GENMOD, SAS 9.2). Gray symbols reflect the numbers of suckling bouts terminated by mother (upper row) and those terminated by the foal (lower row). The figure is based on 1673 bouts recorded in 8 foals of Grevy's zebra, 2080 bouts in 16 foals of plains zebra and 820 bouts in 6 foals in mountain zebra.

($\chi^2 = 8.78$; df $= 1$; $p = 0.003$). Mothers terminated higher rates of suckling bouts in plains zebra (34.4%, $N = 2080$ bouts) than in Grevy's zebra (17.6%, $N = 1673$ bouts; $\chi^2 = 13.77$; df $= 1$; $p < 0.001$) and mountain zebra (24.9%, $N = 820$ bouts; $\chi^2 = 3.93$; df $= 1$; $p = 0.047$). Mountain zebra mothers terminated more suckling bouts than Grevy's zebra mothers ($\chi^2 = 5.51$; df $= 1$; $p = 0.019$). When the mother was feeding while nursing the proportion of suckling bouts terminated by her was lower (23.6%, $N = 1450$) than when she was not feeding (28.1%, $N = 3123$). No other factor including the sex of the foal appeared significant.

4. Discussion

We found that mothers of both species originating from an arid environment (mountain and Grevy's zebras) rejected and terminated a lower rate of suckling bouts/attempts than those of plains zebra, which originally came from a mesic environment. Thus, mothers from the arid adapted species seem to be more tolerant of their foals. This tolerance was most pronounced in Grevy's zebra, and increased with age of the foal. High tolerance by the nursing mother under good nutritional conditions in Grevy's zebra was also recorded in the wild (Rowen, 1993). Reproduction in wild Grevy's and mountain zebras is limited by the environment (Joubert, 1974; Ginsberg, 1989), which results in longer inter-birth intervals in these two species than in plains zebra (Klingel, 1969; Smuts, 1976; Penzhorn, 1985; Penzhorn & Lloyd, 1987; Rowen, 1993; Grange et al., 2004). Our results are apparently in contradiction with parent–offspring conflict theory (Trivers, 1974) suggesting higher conflict when resources are scarce (Festa-Bianchet, 1988). Nevertheless, they may be explained by two possibilities that are not mutually exclusive: (i) foals in the savannah have a more readily available wild diet than in an arid environment, so plains zebras may be rejecting the foals suckling attempts to force them to shift their diet from milk to grass. Mothers in arid environments may delay such forcing because with a poorer wild diet, risk of death, lower growth, etc. is higher than for the same aged foals in a mesic environment. (ii) As a result of their adaptation to poorer habitats, zebras from arid environments may be more efficient in turning food into milk. Thus, either in captivity with a rich diet, or in the wild with abundant food (Rowen, 1993), these mothers may have more milk available for their foals than plains zebra, and probably much more than zebras from arid environments with their standard poor diet.

Our results suggested that parent–offspring conflict in terms of rejection and termination of suckling bouts in the three captive zebra species decreased with increasing age of the foal. This finding is in line with studies of domestic and feral horses (Tyler, 1972; Crowell-Davis, 1985; Crowell-Davis & Houpt, 1986; Barber & Crowell-Davis, 1994; Cameron et al., 2003; Komárková et al., 2011). Thus, parent–offspring conflict in equids seems to be higher in earlier stages of lactation than in later stages. This result contrasts with the parent–offspring conflict theory (Trivers, 1974) which says "as time goes on and the young becomes increasingly capable of feeding on his own (documented by Rogalski, 1973; Martin-Rosset et al., 1978; Carson & Wood-Gush, 1983), the benefit to him of nursing decreases while the cost to his mother may increase". Since suckling bout frequency sharply decreases with increasing age of the foal (Becker & Ginsberg, 1990; Pluháček et al., 2010c), perhaps suckling at a later stage of lactation might mean less discomfort for the mare.

In this respect equids seem to differ from many artiodactyls: in wild boar *Sus scrofa* (Horrell, 1997), pronghorn, *Antilocapra americana* (Byers & Moodie, 1990), impala *Aepyceros melampus* (Mooring & Rubin, 1991), American bison (Wolff, 1988; Green et al., 1993), fallow deer (Gauthier & Barrette, 1985), white tailed deer (Gauthier & Barrette, 1985), or woodland caribou *Rangifer tarandus caribou* (Lavigueur & Barrette, 1992) the proportion of suckling bouts terminated by the mother increases with increasing age of young and/or the majority of suckling bouts was terminated by the mother (e.g., European bison, *Bison bonasus*: Dalezsczyk, 2004; vicuna *Vicugna vicugna*: Vila, 1992; guanaco, *Lama guanicoe*: Sarno & Franklin, 1999; Saharan arrui, *Ammotragus lervia*: Cassinello, 1996). In red deer the increasing conflict over milk supply with increasing age of the calf was even documented by direct measurements of milk production (Landete-Castillejos et al., 2000). Thus, parent–offspring conflict seems to be higher in artiodactyls than in perissodactyls. Such a difference might be based on different physiology, probably resulting from the long evolutionary separation between these two groups of ungulates.

Although maternal care depends on environmental conditions (Bateson, 1994), recent experiments in captive rhesus macaques suggest that conflict-related behavioural traits may be genetically correlated in mothers and offspring (Maestripieri, 2004). Our findings showing interspecific differences in mother-infant behaviour among captive zebras are in line with this suggestion. In ungulates diet greatly affects milk production and composition in both domesticated species like cattle (*Bos taurus*; Oldham & Friggens, 1989), and wild species such as red deer (Landete-Castillejos et al., 2003b). The study on red deer showed that there were differences in milk production and composition between different subspecies under the same diet and housing conditions. These differences could only be attributed to genetic differences and, therefore, should result in differences in behavioural estimators of milk supply. Conversely, in our studies, since all zebras lived in identical climatic environments (with ad libitum food and access to water) and housing conditions, and group composition in terms of sex and age classes was similar, the differences in suckling behaviour could not be affected by a different environment.

Captivity might be an advantageous environment where interspecific differences should be detected; e.g., comparative studies on suckling behaviour of three species of voles (*Microtus ochrogaster*, *M. pinetorum*, *M. pennsylvanicus*: McGuire & Novak, 1984; McGuire et al., 2011), three species of macaques (*Macaca arctoides*, *M. mulatta*, *M. nemestrina*: Maestripieri 1994a, b; *M. mulatta*, *M. tonkeana*, *M. fascicularis*: Thierry, 1985), and two species of suids (*Babyrousa babyroussa*, *Sus scrofa*: MacLaughlin et al., 2000). When several different species are under the same feeding regime and the same living conditions, genetic differences should be indicated (Maestripieri, 2004). In the wild where different species live in different environments it is more difficult to distinguish if a specific behaviour is due to a different genotype (species-specific) or due to living in a different environment.

Equid milk has a low energy content, which implies that mares must produce a large volume of milk to supply the energy needs of their young (Oftedal & Jenness, 1988). Although little fat was found in Grevy's and mountain zebra milk compared to plains zebra, no significant difference has been found in the total milk composition of several captive equid species including all three zebra species in question (King, 1965; Linzell & King, 1966; Oftedal & Jenness, 1988; Schryver et al., 1986). Therefore, milk composition probably cannot explain the differences in suckling behaviour of the three zebra species. Nevertheless detailed research on milk production and composition in zebra species to assess potential differences may complement our study and should be very interesting.

We observed genetic differences in suckling behaviour that could not be attributed to different diet. The mother-offspring conflict (in terms of rejection and termination of suckling bouts among captive animals) was lower in species adapted to arid environments than in a less arid-adapted species. Nevertheless, it should also be noted that since all three zebra species have been maintained in a less arid captive condition than in the wild, mothers in the wild might not be as tolerant toward their foals as the mothers living in captivity in the present study.

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4. Effect of social system on allosuckling and adoption in zebra

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Effect of social system on allosuckling and adoption in zebras

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Abstract

Although nursing non-filial offspring (allonursing) represents costly behaviour to the female, it occurs in a variety of taxa, including ungulates. The only three currently existing species of zebra differ in their ecology and social system. In the wild, mountain zebra *Equus zebra* and Grevy's zebra *Equus grevyi* live in arid environments, while plains zebra *Equus quagga* inhabit savannahs. Mountain and plains zebra mares form long-term stable herds associated with a social hierarchy, whereas Grevy's zebra mares form loose associations of short duration. In this study, we investigated the occurrence of allosuckling in three zebra species at the Dvůr Králové Zoo, Czech Republic, during 1626 h of observation. We recorded no successful allosuckling bouts and only 1 and 22 attempts to allosuckle by foals of mountain and plains zebra, respectively, whereas we observed 117 attempts and 13 successful allosuckling bouts by Grevy's zebra foals. Moreover, more than half of all observed Grevy's zebra foals succeeded in allosuckling at least once. When rejecting an allosuckling attempt, Grevy's zebra mares were less aggressive than mountain and plains zebra mares. When a Grevy's zebra mare allowed occasional allosuckling by a non-filial foal, the probability of long-term allosuckling was smaller than that in mountain and plains zebra. We also present the first evidence of adoption in Grevy's zebra. We suggest that higher tolerance towards non-filial offspring, including the occurrence of allosuckling in Grevy's zebra, was affected by the different social systems of zebra species.

Introduction

Lactation is the most energetically costly part of parental investment for mammals (Oftedal, 1985; Clutton-Brock, 1991). Nursing of non-filial offspring (allonursing) is the most extreme form of communal parenting among mammals (Packer, Lewis & Pusey, 1992). Among ungulates, allonursing occurs in artiodactyls (water buffalo *Bubalus bubalis*: Murphey *et al*., 1995; red deer *Cervus elaphus*: Bartoš *et al*., 2001; Drábková *et al*., 2008; cattle *Bos taurus*: Víchová & Bartoš, 2005; guanaco *Lama guanicoe*: Zapata, Gonzalez & Ebensperger, 2009*b*), but is rare in equids. All reported cases of allonursing in equids involved adoption of a non-filial foal (two cases in wild mountain zebra *Equus zebra*: Lloyd & Harper, 1980; Penzhorn, 1984; two in captive plains zebra *Equus quagga*: Pluháček, Bartošová & Bartoš, 2011; one in wild Asiatic ass *Equus hemionus*: Rashek, 1964; and one in feral horses *Equus ferus caballus*: Cameron *et al*., 1999*a*). Excluding adoptions, allonursing has not been observed in equids. Horse foals were observed to make intention movements of nursing at the flank of a mare other than its mother, but no foal was ever observed to successfully allosuckle (Tyler, 1972; Feist & McCullough, 1976; Crowell-Davis, 1985).

Various equid species and horse breeds differ in suckling behaviour (Carson & Wood-Gush, 1983). The differences in suckling bout duration and frequency may be an adaptation to an arid environment (Becker & Ginsberg, 1990), as Grevy's zebra *Equus grevyi* foals spent the least amount of time suckling and had the longest intervals between suckling bouts compared to plains zebra and horses. In the wild, mountain and Grevy's zebra *E. grevyi* live in an arid environment (semi-deserts), while plains zebra inhabit more mesic savannah (Klingel, 1975; Estes, 1991).

Among artiodactyls, allonursing has been reported in species inhabiting both arid (guanaco: Zapata *et al*., 2009*a,b*; Dromedary camel *Camelus dromedarius*: Gauthier-Pilters & Dagg, 1981; Saharan arrui *Ammotragus lervia*: Cassinello, 1999) and mesic (waterbuck *Kobus defassa*: Spinage, 1969; fallow deer *Dama dama*: Ekvall, 1998) environments. The occurrence of allonursing may be influenced by social structure, as reported for red and fallow deer (Ekvall, 1998; Landete-Castillejos *et al*., 2000). While in populations forming socially stable herds allonursing takes place frequently, it has not been recorded in populations with an unstable group structure (Ekvall, 1998). Most ungulate species with frequent observations of allonursing form closely related stable groups (Lee, 1987; Plesner Jensen *et al*., 1999; Víchová & Bartoš, 2005; Zapata *et al*., 2009*a,b*).

In this study, we compare differences in allosuckling (suckling from a non-maternal female) among three zebra species kept in the same zoo. Our study examines whether allonursing in zebras could be explained by differences in social structure as well as by different environments where the species evolved. In addition to this, we also report the first observation of adoption and allosuckling behaviour in Grevy's zebra and the first records of allosuckling unaffected by adoption in equids. Finally, we discuss our findings in the light of functional hypotheses explaining allosuckling.

Materials and methods

Animals

We observed three zebra species (29 foals and 23 mares of plains zebra in three herds, 8 foals and 18 mares of Grevy's zebra in one herd, and 6 foals and 9 mares of mountain zebra in one herd), at the Dvůr Králové Zoo, Czech Republic. The size of the enclosures ranged from 800 to 2800 m^2. The size of the stable for each herd ranged from 62 to 194 m^2. All observed mares were born at the Dvůr Králové Zoo and the social history of all three species did not differ, excluding individual housing of mountain zebra. The zebras were stabled during the night from October to April. Plains and Grevy's zebras were stabled in groups. Mountain zebra mares were stabled individually; therefore, they were not observed in stables. In the summer, all herds were left in the enclosure 24 h a day. Almost no vegetation was present in any of the enclosures. Fresh food was provided daily *ad libitum* usually in the morning. Several feeding stations were in each enclosure or stable.

Plains zebras were observed from January 1999 to March 2002. All three species were observed from September 2008 to July 2010. Two observers (M. O., J. P.) performed the observations in four different sessions each week using the same methods as Pluháček *et al*. (2007), Pluháček, Bartoš & Bartošová (2010*a*), Pluháček, Bartošová & Bartoš (2010*c*). Both observers observed all herds. Individuals were identified by their unique striping pattern. In each observation session, we collected all data concerning any suckling event.

We used the same definitions of suckling bout, suckling attempt and interruption as other authors studying suckling behaviour of equids (Becker & Ginsberg, 1990; Cameron *et al*., 1999*b*). A suckling bout was regarded as successful when it lasted longer than 5 s and was not interrupted for longer than 60 s. If the interruption of a suckling bout was longer than 60 s, it was considered two suckling bouts. Suckling attempts were defined when suckling lasted for less than 5 s or when foals approached their mothers and the mothers walked away or did not allow the foals to make contact with the teats. We recorded the following data for each suckling bout or suckling attempt: the foal's and mother's identities; the animal that initiated (foal or mother), terminated or interrupted (foal, mother, other herdmate or disturbance by people) a suckling bout; the duration of the bout (in seconds); and the length of interruption within a suckling bout (5–60 s). Allosuckling bouts and allosuckling attempts were also measured when a non-filial foal was involved.

The position of the suckling foal in relation to the mare was recorded as reverse-parallel, perpendicular to the mare or parallel, in line with other studies (Tyler, 1972; Crowell-Davis, 1985). All other data concerning the animals (i.e. date of birth of the foals and parents, number of previous foals of the mother) were obtained from curators of the Dvůr Králové Zoo. The founders of the captive herds were imported to the zoo from the wild in the 1970s, with a detailed pedigree of each individual kept in a zoo recorded studbook.

Each session was performed from either 08:00 to 11:00 h or from 14:00 to 17:00 h on Saturday or Sunday, thus lasting 180 min. This timing includes peaks of suckling activity found in wild and feral equid populations (Joubert, 1972). All data were collected on a voice recorder. In total, we carried out 1626 h of observation (542 sessions over 358 days). The respective herds were observed for 549 h (plains zebra herd 1), 489 h (plains zebra herd 2), 198 h (plains zebra herd 3), 270 h (Grevy's zebra) and 120 h (mountain zebra).

Statistics

All data were analysed using the SAS system, Version 9.2 (SAS Institute Inc., Cary, NC, USA). To compare occurrence of allosuckling among the three zebra species, we used chi-square and Fisher's exact tests. We defined the rate of allosuckling events as the sum of the total number of allosuckling attempts and allosuckling bouts divided by the total number of suckling attempts and bouts. We then compared the rate of allosuckling events among species.

To examine the association between allonursing and relatedness in the Grevy's zebra herd, we first calculated Wright's coefficient of relationship (r) (Wright, 1922) for each foal – mare dyad based on studbook data. Using a general linear mixed model (GLMM, PROC MIXED, SAS) we tested whether relatedness affected the number of allosuckling bouts or allosuckling attempts refused by the mare for each dyad. Dyads involving mother and offspring were excluded from these analyses; we also excluded data of an orphaned and, consequently, adopted Grevy's zebra foal ('Kevin') from before his mother died. To account for repeated measures of the same mare, identity of the mare was entered in the GLMM as a random factor.

Lastly, we compared the duration, frequency, refusal and termination of suckling bouts by the orphaned Grevy's zebra foal to all other Grevy's zebra foals. Because Kevin was orphaned at the age of 182 days, we excluded data of all suckling events of all foals younger than 185 days from these analyses. In the wild, Grevy's zebra foals are weaned from 11 months old (Becker & Ginsberg, 1990). We used the same statistical methods as in our previous study (Pluháček *et al.*, 2011); factors influencing the rejection and termination of suckling bouts by the mother were tested using the logistic regression model (LR, GENMOD procedure) and those affecting suckling bout duration and frequency were tested using a multivariate GLMM. As in other studies (Cameron *et al.*, 1999*a*; Pluháček *et al.*, 2011), we focused on differences among individual foals. Tested factors (independent variables) were the identity of the foal, the foal's age, whether the mother was feeding during the bout (see Pluháček *et al.*, 2010*b*) and the individual terminating the bout (in analysis of suckling bout duration only). To account for repeated measures, the identity of the foal nested within the date was entered as a random factor in the GLMM and as subject in the repeated statement in GENMOD models.

Results

Comparison of allosuckling incidence among three zebra species

In total, we recorded 1 allosuckling attempt in mountain zebra, 22 allosuckling attempts by 11 individual foals from 10 lactating individual mares in plains zebra, and 117 allosuckling attempts by seven individual foals from eight lactating individual mares in Grevy's zebra (excluding the case of adoption). We recorded 13 successful allosuckling bouts from seven individual Grevy's zebra mares, while no allosuckling bouts were observed in plains or mountain zebra (Table 1). Each of the observed Grevy's zebra foals attempted to suckle at least 20 times from one to five different mares and five out of eight foals succeeded in allosuckling at least once. In 7 out of 13 cases, the allosuckling occurred simultaneously with suckling by the filial foal. Average success rate was 10%. Seven mares allowed successful allosuckling bouts; three of them allonursed more than one foal and two of these mares nursed each other's foals.

When we compare the incidence of allosuckling bouts and attempts among all three zebra species, excluding those of the adopted foal, we found a higher number of allosuckling attempts refused by the mare in Grevy's zebra than in plains ($\chi^2 = 38.18$; $P < 0.001$) or mountain zebra ($\chi^2 = 310.75$; $P < 0.001$; Table 1). Similarly, the rate of allosuckling events was higher in Grevy's zebra than that in plains ($\chi^2 = 292.078$; $P < 0.001$) and mountain zebra ($\chi^2 = 54.67$; $P < 0.001$). While in plains and mountain zebra all allosuckling attempts were terminated by the mare kicking, Grevy's zebra mares refused non-filial foals more by moving away (52 cases) than by kicking (44 cases; difference between species – Fisher's exact test $P = 0.012$).

Table 1 Comparison of successful suckling bouts and unsuccessful attempts refused by mother and non-mother among three zebra species

	Mother		Non-mother	
Species	Unsuccessful attempts	Successful suckling bouts	Unsuccessful allosuckling attempts	Successful allosuckling bouts
Grevy's	824	1729	117	13
Mountain	296	843	1	0
Plains	3192	4614	22	0

Bouts and attempts by the orphaned foal are excluded.

Kinship analysis of allonursing in Grevy's zebra

The number of allonursing bouts per mare-foal dyad was affected by kinship [$F = 5.00$; degrees of freedom (d.f.) = 1, 47; $P = 0.030$], but not by the coefficient of relationship of the dyad ($F = 2.45$; d.f. = 1, 47; NS). Conversely, the number of allosuckling attempts refused by the mare per dyad was not affected by kinship ($F = 3.23$; d.f. = 1, 47; NS) or by coefficient of relationship of the dyad ($F = 0.55$; d.f. = 1, 47; NS).

Position of foal during allosuckling

Most suckling bouts of filial foals occurred in the reverse-parallel position (Grevy's zebra: 91%, $n = 1729$; plains zebra: 97%, $n = 4614$; mountain zebra: 94%, $n = 843$). Unsuccessful allosuckling attempts also used this position very often (Grevy's zebra: 32%, $n = 117$; plains zebra: 86%, $n = 22$; mountain zebra, 100% $n = 1$). Successful allosuckling bouts by Grevy's zebra foals were in reverse-parallel, perpendicular to the mare and parallel position (7, 2 and 4 cases, respectively). Only two (Alf and Kevin) out of five foals allosuckled in a parallel position. Each Grevy's zebra foal attempted to allosuckle from every possible position at least once.

Case report of adoption and allosuckling in Grevy's zebra

The male foal 'Kevin' was born to the 21-year-old mare 'Šárka2' on 1 October 2008. He was her 9th foal. Šárka2 died from colic when Kevin was 6 months and 2 days old. Following her death, he successfully suckled from other nursing mares, mainly the 8-year-old primiparous mare 'Tabia', who was also nursing her own female foal ('Belinda'). Kevin successfully survived without any intervention by keepers and was transported to another zoo when he reached the age of 27 months and 13 days.

In total, we recorded Kevin in 100 successful allosuckling bouts; he was unsuccessful in 86 attempts (46%). The rejection rate was much higher than for any other foal's suckling (rate of refused suckling attempts per bout ranged from 14 to 25% for filial foals; $\chi^2 = 51.64$; d.f. = 7; $P < 0.001$; Fig. 1a). Belinda did not allosuckle more than other foals.

We found that the suckling bout duration differed among individual foals ($F = 13.37$; d.f. = 7, 661; $P < 0.001$; Fig. 1b). Kevin's suckling bouts were shorter than bouts of all other foals. Belinda's suckling bout duration did not differ from that of most other foals. When Kevin suckled separately (62 cases out of 100), the suckling bout duration was shorter than when

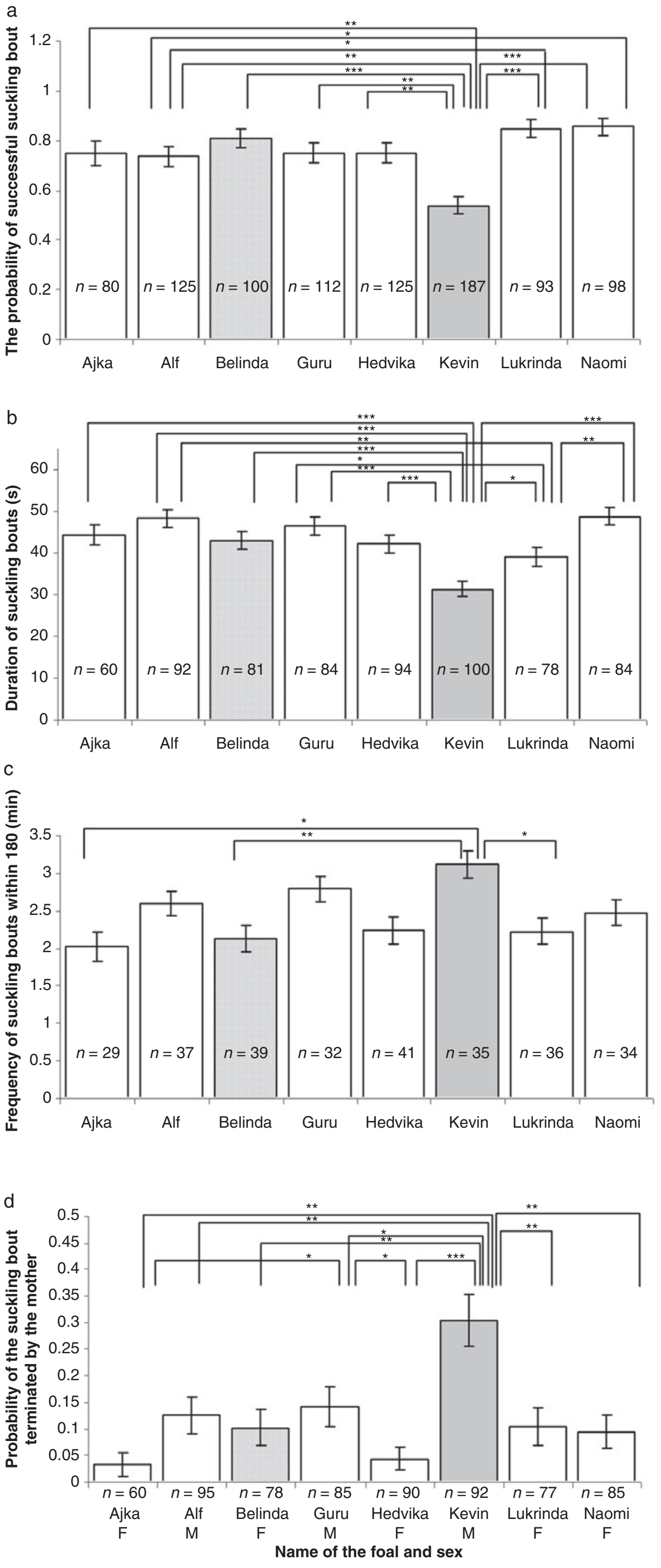

Figure 1 Suckling behaviour of two captive Grevy's zebra *Equus grevyi* foals (filial Belinda and non-filial Kevin) nursed by a mare female (Tabia) compared with control single foals reared in the same herd and season (Ajka, Alf, Guru, Hedvika, Lukrinda, and Naomi). (a) The probability of successful suckling (not rejected by the mare), (b) the suckling bout duration (mean ± SE), (c) the frequency of suckling bouts (within 180 min) and their differences between Kevin and other male or female foals, and (d) the probability of the suckling bouts terminated by the mare. Non-significant differences are not shown. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

he suckled together with another foal ($F = 4.04$; d.f. = 98; $P = 0.047$; Fig. 2). On the other hand, the suckling bout duration of Belinda was not affected by the number of foals simultaneously suckling from her mother ($F = 2.59$; d.f. = 1, 74; NS).

The incidence of interruption initiated by the mare during a suckling bout did not differ among individual mares ($\chi^2 = 8.00$; d.f. = 6; NS) nor among individual foals ($\chi^2 = 8.48$; d.f. = 7; NS). The frequency of successful suckling differed among individual foals ($F = 13.37$; d.f. = 7, 267; $P = 0.010$) and was affected by the interaction between individual foal and its age ($F = 13.37$; d.f. = 7, 267; $P = 0.030$). Kevin allosuckled more frequently than most female foals, but not male foals suckled (Fig. 1c).

Allosuckling bouts by Kevin were more often terminated by the mare than when nursing their own foals ($\chi^2 = 35.32$; d.f. = 7; $P < 0.001$; Fig. 1d). The rate of bouts terminated by the mare was affected by the number of foals suckled at a time. Suckling bouts with two foals at a time were terminated by the mare more often (21%; $n = 92$ bouts) than bouts with only one foal (11%; $n = 570$ bouts; $F = 4.21$; d.f. = 7; $P = 0.040$) regardless of whether the foal was hers.

Discussion

These are the first observations of allosuckling in equids (excluding cases of individual adoption). While mountain and plains zebra foals rarely and unsuccessfully attempted to allosuckle, Grevy's zebra foals attempted and succeeded in allosuckling more often: more than half of them succeeded at least once. Excluding the orphaned foal, three mares allowed suckling from five non-filial foals. When rejecting a non-filial foal, Grevy's zebra mares moved away or kicked the foal at the same frequency, whereas mountain and plains zebra mares terminated suckling attempts by a non-filial foal exclusively by kicking. Thus, our results show higher tolerance of mares towards non-filial foals in Grevy's zebra than in the two other zebra species.

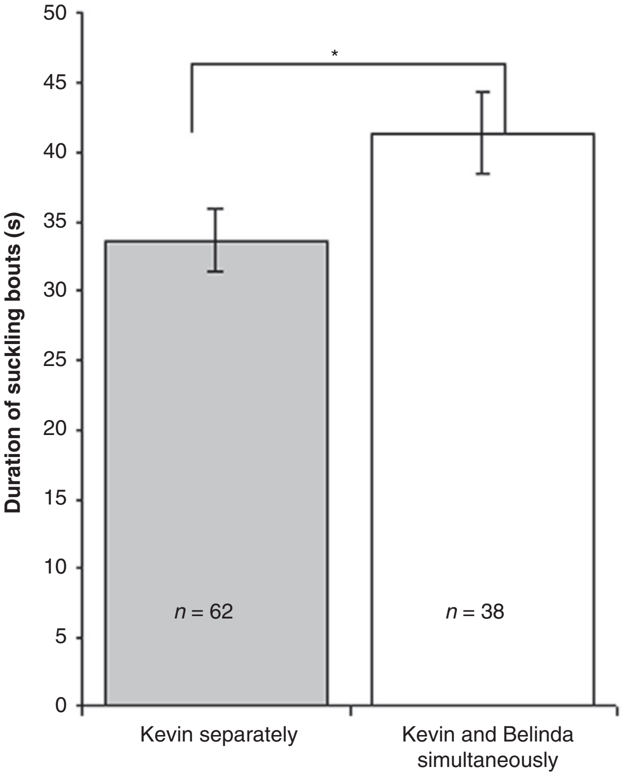

Figure 2 Comparison of the duration of suckling bouts by a mare (Tabia) involving one or two foals at the same time (mean ± SE). *$P < 0.05$.

In the wild, Grevy's zebras inhabit an arid environment (Ginsberg, 1989; Bauer, McMorrow & Yalden, 1994). As nursing creates a high water demand, allonursing could be more expensive in an arid than in a mesic environment. Therefore, higher tolerance of allosuckling in arid dwelling species cannot be explained as an ecological adaptation. However, it might be explained by the different social system of the three zebra species (Klingel, 1974, 1975; Penzhorn, 1979; Linklater, 2000). While mountain and plains zebra females live in stable groups involving a social hierarchy with very little immigration or emigration (Klingel, 1969, 1975; Smuts, 1976; Penzhorn, 1979), Grevy's zebra females form loose associations that only last for a few hours to several days (Ginsberg, 1989; Sundaresan *et al.*, 2007), although some mares with foals can associate with other mares for 2–3 months (Becker & Ginsberg, 1990). In this fission-fusion society, if a Grevy's zebra mare allowed occasional allosuckling by a non-filial foal, the probability of this happening continuously would be limited to a short period. In contrast, in mountain and plains zebra, allosuckling could be prolonged for months as mares and foals remain together in the same group. Therefore, allonursing could ultimately become more expensive for female mountain and plains zebra than for female Grevy's zebra. It should be noted that differences in the social life of female zebra persist in captive or semi-captive conditions (Berger, 1988; Schilder, 1992; Pluháček, unpublished data). The social structure of zebras we observed was very similar to that reported in the wild (Klingel, 1969, 1974; Penzhorn, 1979); for example, we have been able to determine a social hierarchy in plains and mountain zebra, but no social hierarchy was developed in Grevy's zebra despite several generations in captivity (Pluháček, unpublished data).

Allonursing in monotocous species has previously been explained by six hypotheses in terms of cost to the female (Hayes, 2000; Roulin, 2002): kin selection, reciprocity, the parenting hypothesis (females nurse non-filial offspring to improve their maternal skills), the milk theft or evacuation hypotheses, misdirected parental care and the non-adaptive hypothesis. In contrast to studies on allonursing in ungulates (Lee, 1987; Rapaport & Haight, 1987; Cameron *et al.*, 1999*a*; Roulin, 2002), we did not find strong support for the kin-selection hypothesis. An incidence of allonursing in Grevy's zebra was affected by kinship, but not by coefficient of relationship. Our results tentatively seem to support the reciprocal hypothesis as allosuckling was allowed by three mares whose filial foals successfully allosuckled from other mares (Roulin, 2002). Species living in a more stable social organization, such as mountain and plains zebra, would have a greater chance to interact, and so reciprocate. Our findings are in contrast to this, although we cannot rule out the influence of the artificial nature of our study herd due to captivity. Our results are not in line with the parenting hypothesis because we recorded allonursing by multiparous Grevy's zebra mares. Nevertheless, we cannot exclude the milk evacuation hypothesis (Riedman & Le Boeuf, 1982; Wilkinson, 1992), the misdirected parental care hypothesis (Cassinello, 1999; Zapata *et al*., 2009*a*) or the non-adaptive hypothesis (Hayes, 2000) as the possible explanations of allonursing in captive Grevy's zebra.

Allonursing is highly beneficial to the young; however, the milk theft hypothesis is not supported by our data (Landete-Castillejos *et al*., 2000; Maniscalco *et al*., 2007; Zapata *et al*., 2009*a,b*) as foals successfully allosuckled in the reverse-parallel position or perpendicular to the mare. In these positions, the mare can easily check the identity of the foal. Several studies indicate a compensatory function of allosuckling by infants: suckling from non-maternal females as well as from their mothers (Bartoš *et al*., 2001; Víchová & Bartoš, 2005; Zapata *et al*., 2010). Overall, compensation seems to be the most parsimonious explanation for our findings.

Our results came from captive conditions where all three species have *ad libitum* access to food and water. Allonursing is more common in captivity (Packer *et al*., 1992) due to access to unlimited food as well as limited space conditions, which may preclude females from successfully avoiding non-filial offspring attempting to suckle. Therefore, under natural environmental conditions, incidences of allonursing in zebras could be more limited. On the other hand, it should be noted that allonursing in captive ungulates does not seem to be a result of the animals being held in a fenced area (Birgersson, Ekvall & Temrin, 1991). The occurrence of allonursing has been suggested in wild Grevy's zebra in the past (Packer *et al*., 1992). Furthermore, effect of captivity in terms of *ad libitum* access to food and water does not explain why we have only observed allonursing in one out of three zebra species kept under the same conditions.

We recorded the first case of adoption and continuous allonursing in Grevy's zebra. When this case is compared with the similar one reported previously in plains zebra (Pluháček *et al*., 2011), the orphaned Grevy's zebra foal succeeded in allosuckling from all lactating females in the herd, whereas in the plains zebra case, the foal only allosuckled from a single adoptive mare. Similar to the orphaned plains zebra, the orphaned Grevy's foal had more rejected suckling attempts and had shorter suckling bouts, which were more often terminated by a mare than those of filial foals. In contrast to the case of plains zebra adoption, the orphaned Grevy's foal attempted to suckle more often and allosuckled more frequently than filial foals.

In this study, the filial foal of the mare most frequently allosuckled by the orphan foal was no different from other foals in rejection of suckling attempts, suckling bout frequency and duration compared with other foals in the herd, contrasting with the plains zebra case. Apparently, adoption in captive Grevy's zebra did not restrict intake by the filial foal.

The non-filial Grevy's zebra foal was orphaned at the age of 6 months a long time after the sensitive period for mare-foal recognition. In the case of the plains zebra, the second foal was orphaned at the age of 5 months, did not get adopted and did not successfully allosuckle despite the presence of three lactating mares in the herd at the time (Pluháček *et al*., 2011). Thus, we suggest that adoption in Grevy's zebra was facilitated by the higher tolerance of mares towards non-filial offspring found in this species.

Based on the results of our study and in line with the other study (Ekvall, 1998), we can conclude that social system of females could be an important factor affecting the incidence of allonursing in ungulates.

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5. Laterality of suckling behaviour in three zebra species

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Laterality of suckling behaviour in three zebra species

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Although side preference while suckling is an easily characterised lateralised behaviour, few studies have been conducted. We observed laterality in suckling behaviour in three captive zebra species to test two hypotheses: laterality affected by the foal (motor laterality) and laterality affected by the mother. In total we observed 35 foals of Grevy's, plains, and mountain zebra in two zoos and recorded 5128 successful suckling bouts and 9095 unsuccessful suckling attempts. At the population level the only factor affecting side preference of suckling bouts and attempts was the identity of the individual foal. Ten foals showed individual preferences: seven foals preferred suckling from the left side of the mother, three preferred suckling from the right side of the mother. The individual preferences increased with increasing age of the foal. Only one foal was refused more often from the opposite side than the preferred side used for suckling whereas three other foals were refused from the preferred side. Foals that preferred suckling either from left or right side were refused by the mare more often than foals which showed non-preference. Thus lateral preferences in suckling behaviour of zebra foals seem to be in line with the motor laterality hypotheses.

Keywords: Laterality; Suckling behaviour; *Equus*; Zebra.

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Interest in lateralised behaviour in animals has increased in recent years (Austin & Rogers, 2012; Sankey, Henry, Clouard, Richard-Yris, & Hausberger, 2011; Wells & Millsopp, 2009). Lateralised behaviour is thought to reflect brain asymmetries (MacNeilage, Rogers, & Vallortigara, 2009; Rogers, 2010). Research on a range of species has shown that the left hemisphere controls well-established patterns of behaviour performed in non-stressful situations, whereas the right hemisphere responds to unexpected stimuli and controls escape and other emergency responses (Rogers, 2010; Sankey et al., 2011). Perception by an eye is related to contralateral hemisphere, therefore animals (e.g., toads, chicks, or horses) exhibit fear or aggression when a stimulus comes from the left side (Austin & Rogers, 2012; Bisazza, Rogers, & Vallortigara,1998; MacNeilage et al., 2009). Since suckling behaviour contributes to parent–offspring conflict (Pluháček, Bartošová, & Bartoš, 2010; Therrien, Côté, Festa-Bianchet, & Ouellet, 2007; Trivers, 1974), offspring should prefer to approach the female from her right side to prevent maternal aggression before starting to suckle.

Although laterality in teat or side preference while suckling is an easily characterised lateralised behaviour, few studies have been conducted in this area of research. Teat preference has been investigated in primates (Hopkins & De Lathouwers, 2006; Jaffe et al., 2006). Some researchers found a slight left bias in teat preference in certain Old World primates (Damerose & Hopkins, 2002; Hopkins & De Lathouwers, 2006; Nishida, 1993; Tomaszycki, Cline, Griffin, Maestripieri, & Hopkins, 1998). In contrast, other researchers have found a population right teat preference (rhesus monkey *Macaca mulatta*; Lindburg, 1971) or no population preference whatsoever (Japanese macaques *Macaca fuscata*; Hiraiwa, 1981; Tanaka, 1989). On the other hand, several studies (Erwin, Anderson, & Bunger, 1975; Rogers & Kaplan, 1998; Tanaka, 1989) revealed that infants display a strong individual preference for either the left or right teat. Infant age and mother's parity are the factors that appear to have the most influence in laterality of suckling behaviour (Jaffe et al., 2006; Nishida, 1993; Tanaka, 1997). Therefore lateral preferences should be studied on both the population as well as individual level (Damerose & Hopkins, 2002). As recently suggested by Hopkins and Lathouwers (2006), additional longitudinal studies on the interrelationship between early mother–infant asymmetries and development of the offspring should provide important data on the issue.

When suckling, foals most often adopt an anti-parallel position (Figure 1) from which it is able to reach both teats, although it is easier to reach the closer teat. If the foal prefers one teat over the other it should stand by one side of the mother more often to reach the preferred teat better. This type of lateralised behaviour is defined as motor laterality of the foal (McGreevy & Rogers, 2005). In contrast, the mare can prefer to nurse the foal standing along her right side rather than her left side since the left hemisphere of the

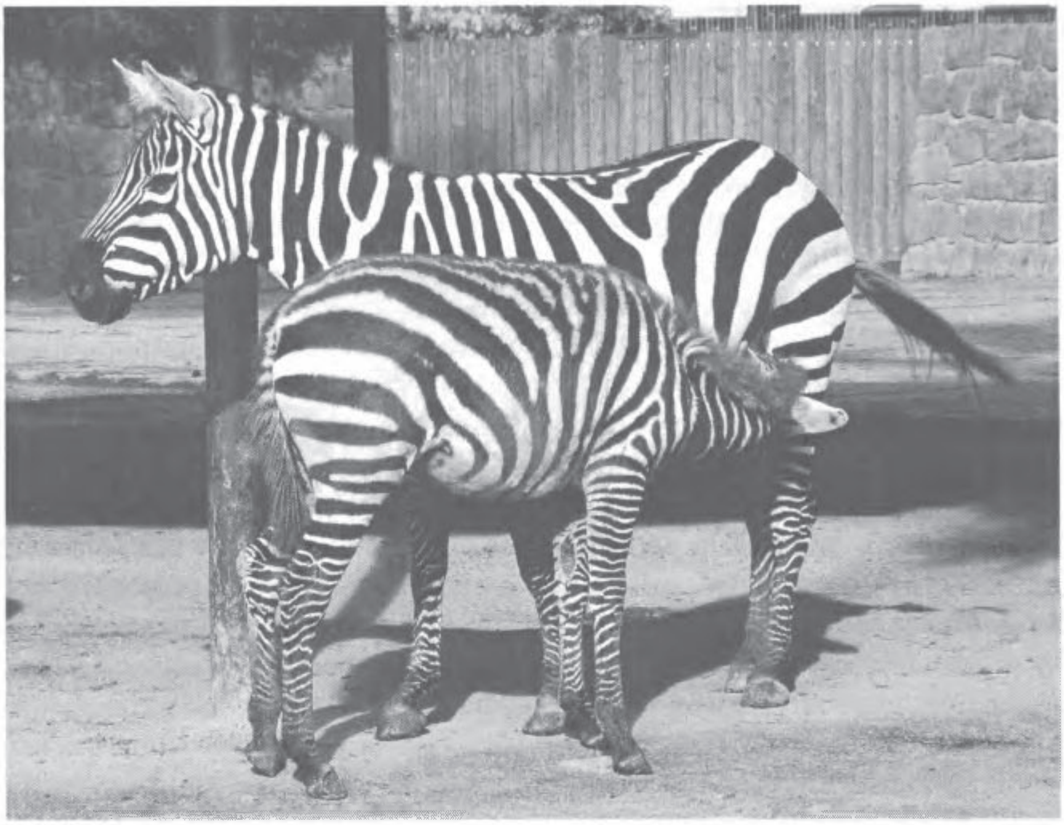

Figure 1. When suckling the zebra foal adopts mostly an anti-parallel position.

brain (affecting the right visual hemifield) controls proactive behaviour and is responsible for positive cognitive bias (Rogers, 2010). Recognition of a mare's own foal is important to prevent allonursing (Cameron, Linklater, Stafford, & Minot, 1999; Lloyd & Harper, 1980; Pluháček, Bartošová, & Bartoš, 2011a). In some mammalian species the female lies down to nurse (Ralls, Kranz, & Lundrigan, 1986), and is therefore responsible for laterality in nursing behaviour; for instance, we recently reported that females of common hippopotamus (*Hippopotamus amphibius*) preferred to nurse while lying on their left side (Pluháček & Bartošová, 2011).

Although suckling behaviour (Barber & Crowell-Davis, 1994; Becker & Ginsberg, 1990; Boyd, 1988; Carson & Wood-Gush, 1983b; Crowell-Davis, 1985; Duncan, Harvey, & Wells, 1984; Feist & McCullough, 1976; French, 1998; Heitor & Vicente, 2008; Martin-Rosset, Doreau, & Cloix, 1978; Rashek, 1976; Rowen, 1993; Smith-Funk & Crowell-Davis, 1992; Tyler, 1972; Waring, 1982) and behavioural lateral preferences (Larose, Rogers, & Ricard-Yaris, 2006; McGreevy, Landrieu, & Malou, 2007; McGreevy & Rogers, 2005; McGreevy & Thomson, 2006; Sankey et al. 2011) have been studied intensively in equids, as far as we are aware only one study refers to side preferences of suckling behaviour in the domestic horse (*Equus caballus*;

Carson & Wood-Gush, 1983a). The researchers reported that the only difference, which occurred when horses were stabled, was that more successful nursing bouts were made from the right side of the dam than from the left side (Carson & Wood-Gush, 1983a). No other difference was reported, including the total number of nursing bouts made from left or right side of the dam. Side preferences have not yet been studied in other equid species.

In the current study we first investigated if foals of three zebra species show any side preferences in suckling behaviour, either on the population level or on the individual basis. We tested two hypotheses: (1) laterality affected by the foal (motor laterality) and (2) laterality affected by the mother. We predicted that if side preference is due to motor laterality then there should be no difference in the side of successful suckling bouts and unsuccessful suckling attempts. On the other hand, if laterality is affected by the mother then the opposite side preference should be recorded for successful suckling bouts than for unsuccessful suckling attempts. Based on previous research in other mammalian species we also explored if side preferences were affected by the sex or the age of the foal, and the species and parity of the mother. Lastly, we tested if suckling bout duration and termination was affected by side of mother along which the foal stood while suckling.

METHOD

Animals

We observed 33 foals (19 plains zebra *Equus quagga* [formerly named *Equus burchellii*], 8 Grevy's zebra *Equus grevyi*, and 6 mountain zebra *Equus zebra*) in five different herds (including three plains zebra herds) at the Dvůr Králové Zoo, Czech Republic and 2 foals of Grevy's zebra at the Ostrava Zoo, Czech Republic (see Table 1). The herd sizes ranged from 2 to 14 breeding mares, aged from 4 to 27 years. All but five of the observed adult mares were multiparous.

In the summer all herds were in enclosures (800 to 2800 m^2) 24 hours a day. From October to April the zebras were stabled at night (stables were 62 to 194 m^2 per herd). Plains and Grevy's zebras were stabled in groups. Mountain zebra mares were stabled individually, therefore they were not observed in stables. There was almost no vegetation present in any of the enclosures. Food was provided *ad libitum* and was given fresh daily, usually in the morning.

Plains zebra at the Dvůr Králové Zoo were observed from September 2001 to March 2002 and from November 2004 to December 2004 (Pluháček, Bartošová, et al. 2010; Pluháček, Bartoš, & Bartošová, 2010; Pluháček,

TABLE 1
Individual side preferences

Species	*Sex of the foal*	*Name of the foal*	*Name of the mother*	*All solicitations (suckling bouts and attempts)*	*Suckling bouts only*	*Suckling attempts refused by the mare*	*Suckling attempts refused by the foal*
Plains	f	Accra	Angelika				
Grevy's	f	Ajka	Arica	*left*			*left**
Plains	m	Akin	Alžběta			left*	
Plains	f	Amina	Alžběta				
Grevy's	m	Alf	Ambra		right*	left	
Grevy's	f	Kora	Barborka				
Grevy's	f	Belinda	Tabia		left		
Mountain	f	Belisa	Bonita			right	
Mountain	f	Brenda	Beata	*left**	*left**	left	*left**
Plains	m	Dario	Desaja				
Plains	f	Galea	Gajda				
Grevy's	m	Guru	Gizela				
Mountain	m	Hasan	Halina	left*	left*		
Grevy's	f	Hedvika	Gobi				
Plains	f	Inet	Irkasa				
Plains	m	Irwin	Irkasa				
Grevy's	m	Fabi	Klára				
Grevy's	m	Kevin	Šárka2	left			left*
Plains	m	Kikwit	Katrin				right
Plains	m	Kim	Kelly		left		
Plains	f	Klea	Kelly				
Mountain	f	Lenka	Lada		right		
Plains	f	Linda	Karolína	*left**	left	left*	left*
Mountain	f	Lola	Linda	right*	right*		*right**
Grevy's	f	Lukrinda	Šelda				right
Mountain	f	Maja	Manka		right		
Plains	f	Miriam	Karmel				
Plains	m	Musarah	Meri	*right**	*right**		
Grevy's	f	Naomi	Nora				
Plains	f	Padme	Penta				
Plains	m	Paris	Palmyra		right*		
Plains	f	Paula	Palmyra	left*	left*		
Plains	f	Penta	Pegy	right*	right*		
Plains	m	Ptolemaios	Piki	*left**	*left**	*left**	*left**
Plains	f	Rubi	Karma		right*		

Individual side preferences when suckling and attempting to suckle in observed foals of three zebra species. Only statistically significant ($p < .05$) preferences are labelled. Preference affected by the age of the foal is italicised.

* Statistically significant also on the level $p < .01$.

Bartošová, & Bartoš, 2011a). All three species were observed at the Dvůr Králové Zoo from September 2008 to July 2010. In Ostrava Zoo Grevy's zebra foals were observed from September 2010 to August 2011. We performed the observations in four different sessions each week. Each session lasted 180 minutes, either from 08h00 to 11h00 or from 14h00 to 17h00 on Saturday or Sunday. This timing includes peaks of suckling activity found in wild and feral equid populations (Joubert, 1972a). For detailed observation methods see Pluháček, Bartoš, Doležalová, and Bartošová-Víchová, 2007, and Pluháček, Bartoš, Bartošová, and Kotrba, 2010. In total we carried out 1254 hours of observation (357 sessions over 196 days). The respective herds were observed for 339 (herd 1 of plains zebra), 330 (herd 2 of plains zebra), 66 (herd 3 of plains zebra), 270 (Grevy's zebra at Dvůr Králové Zoo), 129 (Grevy's zebra at Ostrava Zoo), and 120 (mountain zebra) hours.

In each observational session we collected all data concerning any suckling event. We used the same definitions of suckling bout, suckling attempt, and interruption of suckling bouts as described in previous studies on equids (Becker & Ginsberg, 1990; Cameron, Stafford, Linklater, & Veltman, 1999; Pluháček, Bartošová, et al., 2010). The suckling bout was regarded as successful when it lasted longer than 5 seconds and was not interrupted for longer than 60 seconds. If the interruption of a suckling bout was longer than 60 seconds it was considered as two suckling bouts. Suckling attempts were defined as suckling lasting less than 5 seconds, or cases in which foals approached their mothers and the mothers walked away or did not allow the foals to make contact with the teats using her legs. We recorded the following data for each suckling bout or suckling attempt that was observed: the foal's and mother's identity; the animal that initiated (foal or mother), terminated, or interrupted (foal, mother, other herdmate or disturbance by people [further referred as "disturbance" only]) a suckling bout; the place (stable, yard, enclosure); the duration of the bout (in seconds); and the length of interruption within a suckling bout (from 5 to 60 seconds). The initiator of suckling bout was determined as described by Crowell-Davis (1985). Foals initiated the bout by making intention movement towards the flank of the mother. The mother was initiator when she approached either the resting foal (staying or laying) or the foal engaging in other activity (e.g., playing) and she woke up the foal or stopped its activity. The foal started to suckle immediately. The dominance hierarchy among the adult females was determined by scoring bites and offensive kicking (Pluháček, Bartoš, & Čulík 2006). In each suckling attempt and bout we recorded the side of the mother where the foal stood to suckle.

All observational data were collected using a tape recorder. All other data concerning the animals (i.e., date of birth of the foals and parents, number of previous foals of the mother, etc.) were obtained from curators of the Dvůr Králové Zoo and Ostrava Zoo. We have excluded from all the analyses the following data: suckling bouts ($n = 113$) and attempts ($n = 242$) involving mares other than the mother, suckling attempts terminated due to disturbance or by a herdmate other than a given mother or foal, and successful suckling bouts performed from both sides of the mare.

Statistics

All data were analysed using the SAS System, Version 9.2. First we tested if there was any side preference and factors affecting side preferences. We carried out the analyses in three steps. In the first step we analysed all bouts to see if there was any side preference at the population level. We applied an analysis of categorical repeated measurements based on the generalised estimating equation approach (Liang & Zeger, 1986) using logistical regression (the GENMOD procedure). The explanatory variables were: the foal's age (in days) and sex, the number of dominant mares (at the date of suckling bout or attempt), season (2001/2002, 2004, 2008/2009, 2010/2011), species, mother's pregnancy (yes, no), place where suckling bout or attempt occurred (enclosure, yard, stable), and their first-order interaction terms.

In the second step we focused on side preferences at the individual level using chi-squared tests. If we found that the foal preferred either the left or right side we tested the effect of the age of the foal on side preference using the GENMOD procedure, using the date of observation as a repeated statement.

In the third step we divided all foals into three groups ("left-side-preferring", "right-side-preferring", and "non-preferring") based on previous analyses. We tested if side preference was affected by the species, sex of the foal, or mother's parity using the GENMOD procedure.

All the above analyses were performed separately for successful suckling bouts, for suckling attempts refused by the mother, and for suckling attempts abandoned by the foal.

Additionally we tested if side while suckling or side preference affected suckling bout termination and duration. Suckling bouts terminated by disturbance or herdmate (see Pluháček, Bartošová, et al., 2010) were excluded from these analyses. To test the effect of side or side preference on suckling bout termination we used the GENMOD procedure; the dependent variable was the animal terminating the bout (mother or foal). The explanatory variables were: side position during the bout (left, right), preference of the individual foal (left-side-preferring, right-side-preferring, non-preferring), age and sex of the foal, gravidity and age of the mother, species, season, and place where suckling bout occurred (for details see Pluháček, Bartošová, et al., 2010). To account for repeated measures of the same individuals across the observation period, the analysis was performed with the individual foal as a SUBJECT in the REPEATED statement.

Factors influencing the suckling bout duration were tested using a multivariate general linear mixed model (GLMM, PROC MIXED, SAS; for details see Pluháček, Bartoš, & Bartošová, 2010). We included all the factors tested in our previous studies (Pluháček, Bartoš, & Bartošová, 2010; Pluháček, Bartoš, Bartošová, & Kotrba, 2010), the side position during the bout, and the side preference.

RESULTS

Lateral preferences in suckling bouts and attempts

In total we recorded 5128 suckling bouts (range 45–275 bouts per foal; plains zebra: 2416, Grevy's zebra: 1912, mountain zebra: 800). The mother refused 3143 suckling attempts (range 30–227 attempts per foal; plains zebra: 1944, Grevy's zebra: 906, mountain zebra: 293), and 5939 suckling attempts were abandoned by the foal (range 5–860 attempts per foal; plains zebra: 986, Grevy's zebra: 4433, mountain zebra: 520). The foal stood along the right side of the mother in 2581 (50.3%) suckling bouts, in 1473 (46.9%) suckling attempts refused by the mother and 2764 (46.4%) suckling attempts it abandoned. Almost all suckling bouts were initiated by the foal ($n = 5095$; 99.36%).

On the population level the logistic regression revealed that the only significant factor affecting side preference of all suckling events (bouts and attempts) was the identity of the individual foal, $\chi^2(34) = 126.44$, $p < .0001$. The same factor (individual foal) affected side preference when only successful suckling bouts, $\chi^2(34) = 173.59$, $p < .0001$, suckling attempts refused by the mother, $\chi^2(34) = 53.26$, $p = .0189$, and suckling attempts abandoned by the foal itself, $\chi^2(34) = 58.32$, $p = .0058$ were considered.

When all suckling events were involved we found that 10 out of 35 foals showed a preference for standing either on the left or right side of the mare (Table 1). Seven foals preferred to suckle more often when standing along the left side of the mother, three foals from the right side. In 3 of these 10 foals the side preference grew stronger with increasing age of the foal—Brenda: $\chi^2(1) = 14.48$, $p = .0001$; Musarah: $\chi^2(1) = 12.88$, $p = .0003$; Ptolemaios: $\chi^2(1) = 13.91$, $p = .0002$ (Figure 2).

When considering only successful suckling bouts, seven foals suckled more often when standing along the left side than when standing along the right side of the mother, while for eight foals the opposite was true (Table 1). Four mares were observed in two different (but not subsequent) seasons, each rearing one foal per season. We did not find the same or opposite preference of two foals reared by the same mother (Table 1).

In five foals we recorded more suckling attempts refused by the mother from the left side than from the right; one foal was refused more often when

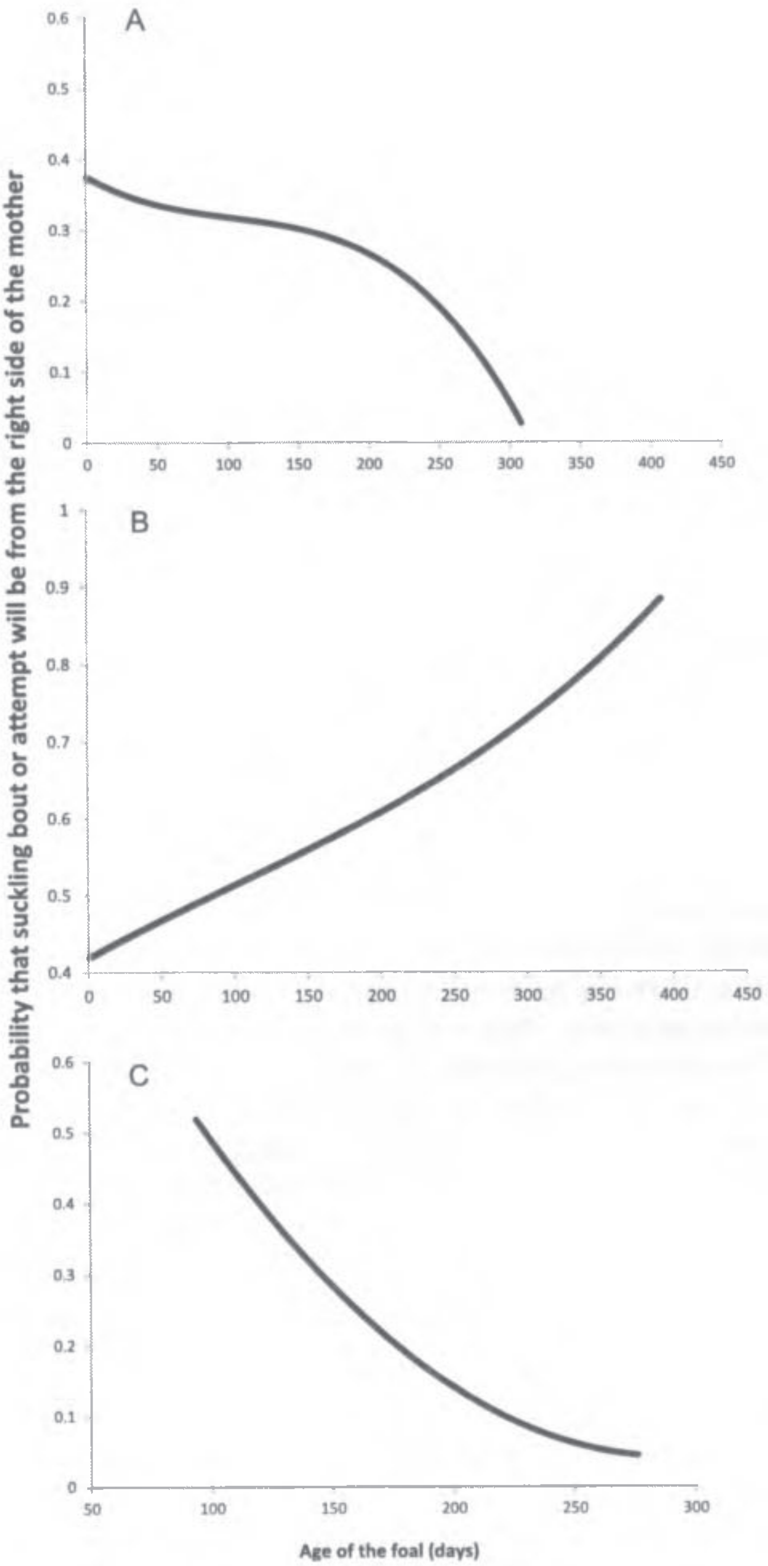

Figure 2. Probability that suckling bout and attempt will occur when standing along the right side of the mother according to the age of the foal in three individual zebra foals: (a) Brenda (mountain zebra, female), (b) Musarah (plains zebra, male), and (c) Ptolemaios (plains zebra, male).

attempting to suckle from the right side. However, only one foal (Alf) was refused more often when attempting to suckle from the side opposite to that where most suckling bouts were recorded (Table 1).

Eight foals showed side preferences in unsuccessful suckling attempts performed and abandoned by the foal itself (Table 1). There was no difference in the foal abandoning attempts from the opposite side than were refused by the mother, or resulted in successful suckling bouts.

What affects lateral preferences of individual foals?

The individual lateral preference was affected by the species (GENMOD), $\chi^2(2) = 6.57$, $p = .038$. We found that mountain zebra foals prefer to stand along one side while suckling more often than Grevy's zebra foals (GENMOD), $\chi^2(1) = 4.92$, $p = .027$. On the other hand, neither the sex of the foal, nor the parity affected side preference of individual foals while suckling. Similarly no effect of species, sex or parity to side preference was found in unsuccessful suckling attempts.

Effect of laterality on rejection, duration and termination of suckling bout

The rejection of suckling bout by the mother was affected by preference shown by individual foals, $\chi^2(2) = 7.16$, $p = .0279$. The non-preferring foals were refused by the mother less often (36%, $n = 5360$ solicitations) than left-side-preferring foals (42%, $n = 1585$ solicitations); $\chi^2(1) = 7.74$, $p = .0054$, and right-side-preferring foals (46%, $n = 849$ solicitations); $\chi^2(1) = 9.47$, $p = .0021$. The interaction between the preference of individual foals and the side where the foal stood when attempting to suckle tended to reach the level of significance, $\chi^2(2) = 7.75$, $p = .0514$. The foals that preferred to stand on the right side were more often refused when they stood by the left side of the mother (55%, $n = 309$ solicitations) than by her right side (42%, $n = 540$ solicitations); $\chi^2(2) = 7.75$, $p = .0001$. No such difference was recorded in left-side-preferring and non-preferring foals.

The suckling bout duration lasted longer when the foal stood along the right side of the mother than when it was along the left side, $F(1, 4682) = 10.16$, $p = .0014$; LS means $\pm SE$: left 55.3 ± 2.12, right 57.2 ± 2.11. Preference of individual foals did not affect the suckling bout duration.

We found that the side affected probability of termination of the suckling bout by the mother, $\chi^2(1) = 4.76$, $p = .0292$. When a foal suckled along the right side, the mother terminated the bout more often (31.1%, $n = 2396$ bouts) than when a foal suckled along her left side (26.6%, $n = 2343$ bouts). Preference of individual foals did not affect the suckling bout termination.

DISCUSSION

We have found that almost one third of observed foals showed individual lateral preference for suckling from one side; 15 foals successfully suckled predominantly from one side; 13 foals showed lateral preference when performing an ultimately unsuccessful suckling attempt. Thus, unlike some studies in primates (Damerose & Hopkins, 2002; Hopkins & De Lathouwers, 2006; Nishida, 1993; Tomaszycki et al., 1998) and in line with other primate studies (Jaffe et al., 2006; Rogers & Kaplan, 1998; Tanaka, 1989) the lateral preferences were observed only on the individual level and not on the population level. Therefore our results show that when studying laterality it is important to distinguish individuals (some studies consider population level only, e.g., McGreevy et al., 2007). The main difference between our study and those on primates is that when standing along one side of the mother, a foal can potentially reach both teats (Carson & Wood-Gush, 1983a; Crowell-Davis, 1985).

We observed that only one foal (Alf; Table 1) was refused more often from the opposite side than the preferred side used for suckling, while three other foals (Brenda, Linda, Ptolemaios; Table 1) were refused from the same side as preferred for suckling. When the same mare nursed two foals in two different seasons we did not see the same lateral preferences in these foals. We found that the rejection of suckling attempts was affected by lateral preferences of individual foals. Mares were more restrictive to foals that tried to suckle more often from one (preferred) side. When a foal approaches from one side more frequently, nursing could be more painful for mares. Thus mares "preferred non-preference of their foals". All these results showing preference either in suckling bouts or suckling attempts are in agreement with the motor hypothesis.

On the other hand, in the case of right-side-preferring foals the preference could be caused by a higher frequency of refusal by the mare when attempting to suckle from the left side. This could support the hypothesis that laterality in suckling is affected by the mother. However, the sample size was limited (only three foals preferred suckling from the right side) and side did not affect the rejection rate in left-side-preferring foals. Thus our results do not to seem favour the hypothesis that laterality in suckling is affected by the mother as revealed in primates (Nishida, 1993). It should be noted that young of primates are altricial and a lot of suckling bouts are initiated by the mother (rhesus monkey: Berman, Rasmussen, & Suomi,1993; great apes: Manning & Chamberlain, 1990; chimpanzee *Pan troglodytes*: Nishida, 1993), as opposed to the precocial young of zebras and horses where almost all suckling bouts and attempts are initiated by the foal (Crowell-Davis, 1985; Tyler, 1972; this study).

In 3 out of 10 foals the lateral preference increased significantly with increasing age of the foal. The strengthening preference over time has been reported in some primates (e.g., macaques: Jaffe et al., 2006) but not all (Hopkins & De Lathouwers, 2006). Our finding is supported by the suggestion that lateral preferences in suckling are a result of visual identification by young as part of the learning process (Jaffe et al., 2006; McGreevy & Rogers, 2005). It should also be noted that it is not clear that lateralised processes, rather than habits acquired at the individual level, are involved in zebra suckling.

Laterality in suckling of zebra foals was not affected by the sex of the foal. Absence of the effect of sex on behavioural laterality has been recorded in neonatal lambs (*Ovis aries*: Lane & Phillips, 2004) as well as in horses (Austin & Rogers, 2012; McGreevy & Rogers, 2005). However, sex differences in suckling behaviour have been reported in plains zebra and in other studies of the domestic horse (Berger, 1986; Duncan et al., 1984; Pluháček, Bartošová, et al., 2010; Pluháček, Bartošová, & Bartoš, 2011b). Sex also did not affect lateral teat preferences in other mammal studies (Damerose & Hopkins, 2002; Hopkins & De Lathouwers, 2006; Jaffe et al., 2006; Nishida, 1993; Tomaszycki et al., 1998).

Various equid species differ in their pattern of suckling behaviour (Becker & Ginsberg, 1990; Pluháček et al., unpublished data) and horse breeds showed differences in motor laterality (McGreevy & Thomson, 2006; Williams & Norris, 2007). In this study most of the mountain zebra foals showed a lateral preference in suckling, while most Grevy's and plains zebra foals did not shown any preference. Within the herd, mountain zebra females are very intolerant towards each other as well as towards unrelated offspring compared to the two other zebra species (Fischhoff et al., 2010; Joubert, 1972b; Lloyd & Rasa, 1989; Penzhorn, 1984; Skalka, 1986). Therefore in mountain zebra the suckling attempt could be more motivated by receiving the mother's protection than in other zebra species. Thus we suppose that a higher lateral preference in suckling behaviour recorded in mountain zebra could be caused by a more intensive learning process of suckling.

Jaffe et al. (2006) found that infant macaques from a primiparous mother had weaker teat preferences than infants of multiparous mothers, and that infants from a primiparous mother developed a side preference earlier than infants of multiparous. In contrast to this study, and in line with others (Hopkins & De Lathouwers, 2006), we did not find any effect of parity on lateral preferences in suckling as well as on development of these preferences over the time.

Mares terminated more suckling bouts performed from their right side than those from their left. This finding is in contrast to our prediction based on the presumption that stimuli coming from the left side induce fear or aggression more than stimuli coming from the right side. Nevertheless it should be noted that horses under experimental conditions showed quick habituation to the repeated stimulus (Austin & Rogers, 2007). Therefore we suppose that bout lateral preference does not play a role after successful start of suckling bout. On the other hand it is necessary to mention that termination is caused by the mare. Mares could use their right limbs better than their left ones to terminate a suckling bout, however we do not know lateral preferences of the observed mares.

Carson and Wood-Gush (1983a) reported no significant difference between mean sucking bout duration on the right or left teat during a successful nursing bout. Our analysis revealed that suckling bouts lasted longer when the foal stood along the mother's right side, however the difference was very small. Therefore we suppose that such a difference has no biological meaning. It should be also noted that suckling bout duration does not reflect milk intake (Cameron, 1998; Cameron, Stafford, et al., 1999). Also we did not find any effect on suckling bout duration of interaction between side, side preference, and the animal that terminated the bout.

Our study is the first report to reveal lateral preference in suckling behaviour among ungulates. Since knowledge of laterality has particular relevance for handling, training, and welfare of animals (Austin & Rogers, 2012; Rogers, 2010), and as lateral preference displays are easily characterised during suckling behaviour (Damerose & Hopkins, 2002; Hopkins & De Lathouwers, 2006; Jaffe et al., 2006), further studies on laterality in suckling behaviour of other ungulate species are needed.

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6. CONCLUSIONS

When combined the results of all individual papers included in this dissertation altogether, I found interesting characteristics of mother-infant behaviour for each zebra species. I could compare these finding all together.

Grevy's zebra foals had the shortest suckling bouts, the lowest frequency, the rate of termination and rejection was lowest of all species, the rate of allosuckling attempts as well as successful allosuckling bouts was several times higher than in two other species. In addition, their suckling bouts were a bit more synchronized than those in plains zebras. All these results showed that the Grevy's zebra mares were the most tolerant to their own offspring as well as to other ones, thus the parent-offspring conflict (Trivers 1974) was least in this species. This tolerance might be associated either with their social organisation (they form loose associations and not closed groups) (Becker & Ginsberg 1990) or it could represent some adaptation to harsh environment (arid one) (Becker & Ginsberg 1990). In arid environment, the high level of parent-offspring conflict can result in higher mortality rate. Thus, higher tolerance towards the offspring can be positively selected. Since Grevy's zebra mothers form loose association (Ginsberg 1988; Becker & Ginsberg 1990), the case of misdirected care cannot be as deleterious as in other species, because the such a care does not last for long time. The high level of allosuckling and synchronisation could be consequence of forming crèche. Thus, the crèche can highly affect the nursing behaviour across the different groups of ungulates. It would be worthy to investigate this effect more deeply in other taxa as well. I would like to point out that to reveal such effect both species - forming the crèche and those not forming the crèche are necessary to investigate. Equids (including zebras) represent such a good group.

Mountain zebras had the highest rate of suckling synchronization compared this phenomenon with other two zebra species. Further, they had the longest suckling bout duration and higher rate of suckling bout frequency than Grevy's zebras. On the other hand, they rejected and terminated suckling bout attempts less than plains zebra. Mountain zebra mare are absolutely intolerant to other foals. Thus, there was no incidence of allosuckling and just one attempt was recorded. It shows very strong bond between mother and foal in this species. It could be caused by high rate of aggression between mares. This tolerance to their own foals and high aggression to other foals and mares seems to be adaptation to an arid environment in which this species naturally lives (Penzhorn 1985).

Plains zebras had the lowest rate of synchronization among these three species. Plains zebra had longer suckling bout duration than Grevy's zebras but shorter than mountain zebras. Plains zebra mares terminated the most suckling bouts between these three species, and they were no tolerant to other foals to allosuckling. I observed more allosuckling attempts in plains zebras than in mountain zebra, although the rate of allosuckling attempts was much lower than in Grevy's zebra foals. This shows stronger bond between mother and foals of plains zebras, but higher intolerance of mares to other foals than Grevy's zebra mares. It seems to be connected to social organization of this species more than to environment adaptation. It would be interesting to compare these characteristics with wild asses, since they inhabit arid environment and their social organisation is very similar to Grevy's zebra.

It seems that laterality of suckling behaviour doesn't exist in these species on population level, just on individual level like among horses (Komárková & Bartošová 2012). There was found just one laterality difference between these three species. Mountain zebra foals preferred to stand along one side more often than Grevy's zebra foal. It could be connected to social organization of these species. As mountain zebra mares had higher aggression rate than Grevy's zebra mares, thus mountain zebra foals can prefer the "safer" side of the mother.

Synchronized behaviour is one of the neglected topics in behaviour ecology. There is no other comparative study about synchronization of maternal behaviour among ungulates. This phenomenon could even work for human babies and females too.

All the studies included in this thesis revealed difference in suckling behaviour and maybe in maternal input in these three zebra species. These results show that suckling behaviour could be affected by social hierarchy and ecology of those three zebra species. For future research, I suggest that it would be interesting to study other wild or captive equid species as wild asses (African wild ass (*E. africanus*) and Asiatic wild asses (*E. hemionus; E. kiang*) and wild horses to carry out. I would like to emphasize the gaps in our knowledge of suckling behaviour in wild asses.). The other topics that might be interesting for comparative studies in equids include resting behaviour or ending of resting, synchronization of resting behaviour, how it is different between these and other equid species. Moreover, the additional important comparative topic could be laterality of other behaviour than suckling in all equid species and their comparisons. Equids especially zebras and asses seem to be very good model species in behavioural ecology studies. I am very pleased that I have had an opportunity to study these species and their behaviour. It was really interesting, fascinating and informative topic.

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8. TABLES

Table 1. Proportion of suckling attempts terminated by the mother, foal, herdmates and disturbance according to the sex of the foal and pregnancy status of the mother in 20 individual foals of plains zebra observed at Dvůr Králové Zoo (Czech Republic) (Pluháček et al. 2010).

Terminated by	Male foals	Female foals	Pregnant mothers	Non-pregnant mothers	Total
Mother	1503 (81.4 %)	576 (75.9 %)	976 (81.0 %)	1103 (78.8 %)	2059 (79.8 %)
Foal	325 (23.5 %)	178 (17.6 %)	222 (18.4 %)	281 (20.1 %)	503 (19.3 %)
Herdmates	15 (0.8 %)	2 (0.3 %)	4 (0.2 %)	13 (0.5 %)	17 (0.7 %)
Disturbance	3 (0.2 %)	3 (0.4 %)	3 (0.3 %)	3 (0.2 %)	6 (0.2 %)
Total	1846	759	1205	1400	2605

Table 2. Proportion of suckling bouts terminated by the mother, foal, herdmates and disturbance depending on the sex of the foal and pregnancy status of the mother in 20 individual foals of plains zebra observed at Dvůr Králové Zoo (Czech Republic) (Pluháček et al. 2010).

Terminated by	Male foals	Female foals	Pregnant mothers	Non-pregnant mothers	Total
Mother	939 (40.8 %)	278 (29.2 %)	675 (40.9 %)	542 (33.8 %)	1217 (37.4 %)
Foal	1298 (56.4 %)	644 (67.7 %)	937 (56.8 %)	1005 (62.7 %)	1942 (59.7 %)
Herdmates	51 (2.2 %)	23 (2.4 %)	31 (1.9 %)	43 (2.7 %)	74 (2.3 %)
Disturbance	13 (0.5 %)	6 (0.6 %)	7 (0.4 %)	12 (0.8 %)	19 (0.6 %)
Total	2301	951	1650	1602	3252

Table 3. Numbers of suckling bouts terminated by the mother, foal, herdmates and disturbance in three zebra species observed at Dvůr Králové Zoo. (Only bouts in non-pregnant mares are included.) (Pluháček et al. 2012)

Terminated by	Grevy's zebra	Mountain zebra	Plains zebra
Mother	294 (17.0 %)	204 (24.2 %)	715 (33.4 %)
Foal	1379 (79.8 %)	616 (73.1 %)	1366 (63.8 %)
Herdmates	31 (1.8 %)	15 (1.8 %)	41 (1.9 %)
Disturbance	20 (1.2 %)	7 (0.8 %)	18 (0.8 %)
Total	1724	842	2140

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9. APENDICES

a. Curriculum vitae of the author

Ing. Michaela Levá (Olléová)
Pelnářova 403, 344 01 Domažlice, Czech Republic
Birth date: 24th December 1986, Náchod
Tel.: (+420) 736 101 315
E-mail: olle.michaela@gmail.com
Marital status: married, 2 children

Experience

2020 – still	Private elementary school and kindergarten Adélka, o. p. s. - teacher
2015 – 2021	Maternity leave
2020 – still	Exercise teacher in the Shakti center of Domažlice
2014 – 2015	Department of Ethology, Institute of Animal Science - assistant
2013 (February – June)	Volunteer for "Carnivore monitoring program" in
Zakouma NP, Chad	
2009 (June – September)	Experience as a keeper in the Zoo Dvůr Králové

Education

2012 -	Czech University of Life Sciences Prague, Institute of Tropics and Subtropics, Agriculture of Tropics and Subtropics (PhD study)
2011 – 2015	Czech University of Life Sciences Prague, Institute of Education and Communication, follow up study of teaching the vocational subjects at the secondary and apprentice schools
Finale state exams	Pedagogy, psychology, didactics of professional
subjects	
Final work	Didactic project in teaching the subject of biology and
ecology	
2010 - 2012	Czech University of Life Sciences Prague, Institute of Tropics and Subtropics, Wildlife Management of Tropics and Subtropics, study in English
Final state exams	Behavioural Ecology, Breeding of Indigenous Animals Species in TS, Animal Population Dynamics
Diploma thesis	Interspecific Characteristics of Suckling Behaviour in Three Zebra Species
2006 – 2010	University of South Bohemia, Faculty of Science,
Biology	
Final state exams	Animal Biology, Physiology and Development Biology of Animals and Plants, Ecology
Bachelor thesis	Factors Affecting Suckling Behaviour in Bovids
2002 – 2006	Náchod's Jirásek Grammar School
	Graduation

Awards

2013	Josef Hlávka's award for the best students and graduates of Prague Universities
2012	Award of Ministry of Agriculture for the best diploma thesis

Publications

Title: Does social facilitation affect suckling behaviour in zebras?
Authors: **Michaela Levá**, Jan Pluháček
Journal: Behavioural Processes, 2021, 185, 104347.

Title: Effect of social system on allosuckling and adoption in zebras
Authors: **Michaela Olléová**, Jan Pluháček & Sarah B. King
Journal: Journal of Zoology, 2012, 288, 2: 127-134.

Title: Effect of ecological adaptation on suckling behaviour in three zebra species. Behaviour
Authors: Jan Pluháček, **Michaela Olléová**, Jitka Bartošová, Luděk Bartoš
Journal: Behaviour, 2012,149: 1395-1411.

Title: Laterality of suckling behaviour in three zebra species
Authors: Jan Pluháček, **Michaela Olléová**, Jitka Bartošová, Jana Pluháčková & Luděk Bartoš
Journal: Laterality: Asymmetries of Body, Brain and Cognition, 2013, 18, 3, 349-364.

Title: Time spent suckling is affected by different social organisation in three zebra species.
Authors: Jan Pluháček, **Michaela Olléová**, Luděk Bartoš & Jitka Bartošová
Journal: Journal of Zoology, 2014, 292, 1, 10-17.

Conferences

Zoological Days Brno (2015), (presentation)
7th European Conference on Behavioural Biology (2014), (presentation and poster)
Zoological Days (2014), (presentation)
7th Scientific Conference of the Faculty of Tropical AgriSciences (2013), (presentation)
40. Ethological Conference, Košice, SK (2013)
6th Scientific Conference of the Institute of Tropics and Subtropics (2012), (Poster)
38. Ethological Conference, Kostelec nad Černými Lesy (2011), (Poster)
Zoological Days (2009)

Languages

English (active knowledge, C1)
German (passive knowledge, A1)
French (basic knowledge, A1)

Skills

Computer skills – MS office, internet, Statistica, GIS, SAS
Driving license B

Courses

2019	fitMAMI Baby tutoring course "Exercise with infants and toddlers"
2015	The Training course to obtain a qualification and professional competence in the field of experimental animals according to §15d odstavce 2 písmeno a) zákona č. 246/1992 Sb., na ochranu zvířat proti týrání, v platném znění.
2013	The Course of Fundamentals of Scientific Work of the Czech Academi of Sciences
2012	The Ejhle Instructor Course for scout leaders
2020, 2016, 2012, 2008	Continuation of certificate for Medics at recovering Actions
2005	Leader wood course “Stříbrná řeka”
2004	I pass out the course for Medics at recovering Actions

Interests

2019 - still	Voted member of district council - district Domažlice
2017, 2018, 2019-2020	Leader of the educational course for patrol leaders “KRAP"
2016 – still	Chair of the Audit Committee of the Center Jiřinky Paroubkové Domažlice
2016 – 2019	Deputy leader of district council – district Domažlice
2015	Instructor at the educational course for patrol leaders “Filia”
2010, 2014	Leader of the educational course for patrol leaders “Filia”
2011 – 2015	Delegate from Královéhradecký kraj in the Board of Association of Scouts and Guides of the Czech Republic
2013, 2014, 2015, 2016	Instructor at educational course for scout leaders “Polojasno”
2012, 2013, 2014, 2015, 2016	Instructor at educational course for scout leaders “Pračolek”
2011, 2012	Instructor at motivation course for scout patrol leaders “Žirafa Krkonoše”
2010	Member of JK ZF JU České Budějovice
2008 – 2010	Leader at the student's Tea room “U Robinsona” in České Budějovice
2007, 2008	Co-organizer of Ekofilm at Faculty of Science in České Budějovice
2006, 2007, 2009, 2010, 2011, 2013	Leader of summer scout camps, leading accounts
2006 – 2009	Member of “Na Hnízdě” = Association of students at Faculty of Science at the University of South Bohemia in České Budějovice
2006 – 2012	Leader of 2. Girls troop Junák, center Náchod
2000 – 2005	Member of the Horse riding club “Ranč Lipí”
Since 1999	Member of the Junák – Association of Scouts and Guides of the Czech Republic

Abilities

I am capable to be a team leader and a team player too. I have very good computer skills. My opinion is that I am responsible, independent and rigorous.

Domažlice 1st April 2022

b. List of authors papers

1. **Title: Does social facilitation affect suckling behaviour in zebras?**

Authors: **Michaela Levá**, Jan Pluháček

Journal: Behavioural Processes, 2021, 185, 5, 104347.

IF: 1.777

Declaration of contributions:

> ***Michaela Levá:*** Conceptualization, Data curation, Formal analysis, Investigation, Visualization, Writing - original draft.
>
> *Jan Pluháček:* Funding acquisition, Investigation, Methodology, Project administration, Supervision, Validation, Writing - review & editing, Investigation.

2. **Title: Time spent suckling is affected by different social organisation in three zebra species.**

Authors: Jan Pluháček, **Michaela Olléová**, Luděk Bartoš & Jitka Bartošová

Journal: Journal of Zoology, 2014, 292, 1, 10-17.

IF: 2.322

Declaration of contributions:

> *Jan Pluháček:* Funding acquisition, Investigation, Methodology, Project administration, Supervision, Validation, Writing - original draft, Investigation.
>
> ***Michaela Olléová:*** Conceptualization, Data curation, Formal analysis, Investigation, Editing.
>
> *Luděk Bartoš:* Conceptualization, Methodology, Editing, Formal analysis.
>
> *Jitka Bartošová:* Methodology, Formal analysis.

3. **Title: Effect of ecological adaptation on suckling behaviour in three zebra species. Behaviour**

Authors: Jan Pluháček, **Michaela Olléová**, Jitka Bartošová, Luděk Bartoš

Journal: Behaviour, 2012,149: 1395-1411.

IF: 1.991

Declaration of contributions:

> *Jan Pluháček:* Funding acquisition, Investigation, Methodology, Project administration, Supervision, Validation, Writing - original draft, Investigation.
>
> ***Michaela Olléová:*** Conceptualization, Data curation, Formal analysis, Investigation, Editing.
>
> *Jitka Bartošová:* Methodology, Formal analysis.

Luděk Bartoš: Conceptualization, Methodology, Editing, Formal analysis.

4. **Title: Effect of social system on allosuckling and adoption in zebras**

Authors: **Michaela Olléová**, Jan Pluháček & Sarah B. King

Journal: Journal of Zoology, 2012, 288, 2: 127-134.

IF: 2.322

Declaration of contributions:

Michaela Olléová: Conceptualization, Data curation, Formal analysis, Investigation, Visualization, Writing - original draft.

Jan Pluháček: Funding acquisition, Investigation, Methodology, Project administration, Supervision, Validation, Writing - review & editing, Investigation.

Sarah R. B. King: Editing, Formal analysis.

5. **Title: Laterality of suckling behaviour in three zebra species**

Authors: Jan Pluháček, **Michaela Olléová**, Jitka Bartošová, Jana Pluháčková & Luděk Bartoš

Journal: Laterality: Asymmetries of Body, Brain and Cognition, 2013, 18, 3, 349-364.

IF: 0.938

Declaration of contributions:

Jan Pluháček: Funding acquisition, Investigation, Methodology, Project administration, Supervision, Validation, Writing - original draft, Investigation.

Michaela Olléová: Conceptualization, Data curation, Formal analysis, Investigation, Editing.

Jitka Bartošová: Formal analysis, Methodology.

Jana Pluháčková: Investigation.

Luděk Bartoš: Conceptualization.