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DIPLOMA THESIS

Interspecific characteristics of suckling behaviour in three zebra species

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Declaration

I declare that this diploma thesis on the theme: Interspecific characteristics of suckling behaviour in three zebra species, was elaborated independently and is based only on my own knowledge, consultations with my supervisor and literary resources cited in the attached bibliography.

Prague 15th April 2012

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Michaela Olléová

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Abstract

The diploma thesis consists of two manuscripts studying maternal behaviour in three zebra species: plains zebra [*Equus quagga*], mountain zebra [*Equus zebra*], Grevy’s zebra [*Equus grevyi*]. Manuscripts have been sent to peer-reviewed journals. These zebra species differ in habitat adaptations as well as in social organization of herds. Mountain zebra and Grevy’s zebra live in an arid environment in the wild, while plains zebra live on a savannas. Mountain zebra and plains zebra form long-term stable associations with strong social hierarchy, whereas Grevy’s zebra form short-term unstable associations. The study is based on my own observations carried out in Zoo Dvůr Králové nad Labem in years 2008-2010. During these observations (795h) I recorded in total 7 186 suckling bouts, 140 allosuckling attempts (in all three zebra species) and 13 cases of allonursing (mare nursing other foal than her own), (in Grevy’s zebra). Moreover, I observed the adoption of one orphaned male foal in Grevy’s zebra. I found out lower incidence of termination and rejection by the mother in Grevy’s and mountain zebra, than in plains zebra. I suggested the possible explanation for this result is saying that mothers of species from an arid environment are more tolerant to their offspring than mothers of species evolved in a mesic environment. On the other hand, I found out high incidences of allosuckling attempts and allonursing bouts in Grevy’s zebra opposite to other two species, where only few allosuckling attempts and no allonursing were observed. Allonursing occurs very rarely in perissodactylas. The case of adoption I observed was not similar to those reported for other equids species so far. Male foal was at the age of six months when orphaned, therefore enough to survive without nursing. Own foal of mare which allonursed orphaned foal was not rejected more often than other foals and its suckling bout duration was similar as that of all other foals in the herd. Based on the results I presume that allonursing among zebra species is rather influenced by the social organization than by the environmental adaptation.

Key words:
Zebra, suckling behaviour, allonursing, adoption, zoo, social organization, parent-offspring conflict, interspecific comparison

Abstrakt

Tato diplomová práce se skládá ze dvou rukopisů, které se zabývají mateřským chováním u tří druhů zeber (zebra stepní [*Equus quagga*], zebra horská [*Equus zebra*], zebra Grévyho [*Equus grevyi*]), zaslaných do impaktovaných časopisů. Tyto tři druhy zeber se liší jak v habitatové preferenci tak v sociálním uspořádání stáda. V přírodě žije horská zebra a zebra Grévyho v aridních oblastech zatímco zebra stepní žije na savanách. Zebra horská a zebra stepní tvoří dlouhodobě stabilní stáda se striktní sociální hierarchií, kdežto zebra Grévyho tvoří volná krátkodobá uskupení. Výzkum je založen na etologickém pozorování v Zoo Dvůr Králové nad Labem v letech 2008-2010. Během pozorování (795h) bylo zaznamenáno 7 186 kojení, 140 pokusů o alokojení (u všech tří druhů) a 13 případů alokojení (kojení u cizí samice), (u zeber Grévyho). U zeber Grévyho jsem také pozorovala adopci šestiměsíčního samečka. Zjistila jsem, že zebry Grévyho a zebry horské odmítaly a ukončovaly menší množství kojení, než zebry stepní. Tedy předpokládám, že u druhů ze sušších oblastí jsou matky více tolerantní ke svým mláďatům, než matky z mírnějších oblastí. Na druhou stranu jsem zjistila velké množství alopokusů u zeber Grévyho oproti ostatním druhům a také několik úspěšných alokojení. Alokojení je u lichokopytníků velkou zvláštností. Případ adopce, který jsem sledovala, byl odlišný od dosud pozorovaných adopcí u koňovitých. Sameček byl dost starý, aby přežil bez mléka, a vlastní mládě adoptivní samice nebylo odmítáno ani nebylo kojeno kratší dobu než ostatní mláďata. Na základě těchto výsledků se domnívám, že alokojení je u zeber spíše než prostředím ovlivněno sociálním uspořádáním stáda.

Klíčová slova:
Zebry, kojení, alokojení, adopce, zoo, sociální uspořádání, konflikt rodiče a potomka, mezidruhové srovnání

CONTENT

1. INTRODUCTION

1.1. Introduction

It is the first study comparing suckling characteristics of all living zebra species. The work includes the primary study of suckling behaviour about mountains zebra. I considered many aspects of the mother–infant interactions and interspecific characteristics among all zebra species which has never been done. The second part is important due to the first so extant report of allosuckling and allo–attempts among perissodactylas and the first note of an adoption in Grevy's zebra and an adoption of the foal older than three month.

The thesis consists of two manuscripts, which have been submitted to peer-reviewed journals (Animal Behaviour and Journal of Zoology). Analyzes includes also the data of maneless, Grant's and Chapman's zebra which were studied during 1999-2002 years by Jan Pluháček. The allonursing part has been presented at the 38. Czech and Slovak Ethological Conference 2011 as the poster (see appendix 2).

1.2. Aims of the diploma thesis

Main aims of my study are to find out which factors influence suckling behaviour and finally what are the main aspects and differences of allosuckling among three zebra species, namely: Grevy’s zebra (*Equus grevyi*), mountain zebra (*Equus zebra*), and plains zebra (*Equus quagga*). I have tested hypotheses about an ecological adaptations, social live, phylogeny and differences among three zebra species.

Here is the list of tested hypotheses:

1. The suckling behaviour and the incidence of allosuckling behaviour will depend on an environment in which zebra species evolved. Zebras from an arid environment (Grevy’s and mountain zebra) would not be so tolerant to their foals, because they need to save energy more than species evolved in a mesic environment (plains zebra).
2. The suckling behaviour will reflect the social organization of zebra. The suckling bout frequency and total time spent by suckling will increase with increasing competition among mares.
3. The allosuckling behaviour will depend on an environment in which zebra species live. Zebra from an arid environment won’t be more tolerant to non filial foals, because mares save energy for their own offspring.
4. The allosuckling behaviour will depend on the social organization of zebra females. Species form an unstable short-term associations will tolerate non filial foals more than species form a stable long-term associations.
5. Finally, I have discussed my finding of allosuckling in Grevy’s zebra in the light of the hypotheses explaining allosuckling behaviour in view of females (Roulin 2002): the misdirected parental care hypothesis, the reciprocity hypothesis, the kin selection hypothesis, the milk evacuation hypothesis, the parenting hypothesis.

2. BIBLIOGRAPHIC RESEARCH

2.1. Introduction about suckling and nursing

The lactation is the physiological action ending with the secretion of milk (Hall et al. 1993). Milk providing is very important for young. It is both physical and an emotional nourishment and security of the young (Apter & Householder 1996). On the other hand lactation is far more demand for a mare than the whole pregnancy (Gittleman & Thompson 1988; Rogowitz 1998; Sadleir 1984). Young needs much more calories during 1-2 days of a postnatal growth than it needed as the foetus (Blaxter 1971). Milk provides to offspring nutrients, hormones, vitamins and immune compounds (Jensen 1995; Roulin 2003). Equids milk includes 10-12% total solids, 1-2% fat, 1.6-1.8% true protein, 6-7% 'lactose', 0.3-0.5% ash, 0.08-0.12% calcium, 0.04-0.07% phosphorus and if they calculated the energy content it was 2.0-2.4 kJ/g (Oftedal & Jenness 1988). The composition of zebra’s milk is nearly similar to horse (Oftedal & Jenness 1988). For my study is important that all equids species have similar milk content. The maternal influence divides into three major phases: the gestation, the lactation and the post-weaning period of development, if we look on the energy allocation between mother and offspring the most important are the gestation and the lactation (Rogowitz 1998). Weaning is the most conflict time for the mother – offspring interaction (Trivers 1974; Green et al. 1993; Birgersson & Ekvall 1994).

Elder studies assumed that the time spent suckling is equivalent for milk transfer to offspring (Martin 1984, Wettemann et al. 1978). However, if I consider the fact that the observed time spent suckling and the frequency doesn’t check with the amount of energy intake by the foal (Cameron et al. 1999b). I couldn’t test hypotheses about mother – infant conflict with suckling characteristics. Still, I was able to test these hypotheses by the termination and the rejection as per source (Green et al. 1993; Cameron et al. 2000; Cameron et al. 2003). This is the time when the conflict between offspring and mother is really obvious (Trivers 1974; Green et al. 1993; Birgersson & Ekvall 1994). The parent – offspring conflict theory (Trivers 1974) states that offspring wants more energy from the parent, but the parent doesn’t want to invest into the current offspring so much, due to the fact that offspring is more independent with age and parent wants to save energy for another potential offspring. In other words: “The longer the current offspring is nursed, the lower is the probability that the next offspring will survive (Bateson, 1994).” It means that mare should terminate suckling bouts, and suckling attempts sooner and more often with the increasing age of the foal (Green 1990; Cameron & Linklater 2000; Cameron et al. 2000; Cameron et al. 2003).

During my study I recorded every considerable characteristics of suckling behaviour (the suckling bout frequency, the suckling bout duration, the total suckling duration, which animal initiated and terminated the suckling bout, the position of the foal during suckling). These characteristics are usually used for testing sociobiological hypotheses.

Why do I usually use the term suckling? Suckling involves two situations: nursing and sucking. Sucking is used if I look on maternal behaviour from the side of the young. Nursing (nursing bout, nuzzling, nursing frequency, nursing rate) is used from the view of mother. Nurse also means to take care of someone. I consider the term suckling the very suited for the first part of my study where I describe and compare suckling characteristics among three zebra species. On the other hand I use the term allonursing in the second part of the thesis more frequently. Allonursing is more suited for the action of the adoption. Allosuckling attempt is use for case when foal is trying to suckle, other mare than its own.

The tricky and confusing part is how to determine the suckling bout. Below I describe the definitions used for suckling characteristics. A lot of ungulates researchers consider the start of suckling bout at the time when the foal take the udder into its mouth (Barber & Crowell-Davis 1994; Becker & Ginsberg 1990; Cameron et al. 1999a,b; da Costa et al. 2000; Das et al. 2000; Das et al. 2001; Day 1987; Drews 1991; Froberg & Lidfors 2009; Lewandrowski & Hurnik 1983; Mooring & Rubin 1991; Nakanishi et al. 1993; Stewart et al. 1993a; Stewart et al. 1993b; Špinka & Illmann 1992; Underwood 1979; Vandenheede et al. 2001). I started timing the suckling bout when the foal held the udder longer then 5s. The suckling bout was not interrupted longer than 60s, any interruption longer than 5s was noted as a break. If the interruption was longer than 60s, the following suckling was considered as another suckling bout. This definition has been used in other studies (Becker & Ginsberg 1990; Smith-Funk at al. 1992; Barber & Crowell-Davis 1994; Cameron et al. 1999a,b; Crowell-Davis 1985; Pluháček et al. 2010).

The first used characteristic is the total time spent by suckling. It is the period of time spent by suckling set for a specific time. I summed the durations of suckling bouts per specific time as per sources (Das et al. 2000; Das et al. 2001; Day et al. 1987; Green 1990; Green et al. 1993; Nakanishi et al. 1994; Perez-Hernandez et al. 2002). Each session took 180min and was done during the weekends. Another suckling characteristic is suckling bout frequency. It is number of suckling bouts per time (Das et al. 2000; Das et al. 2001;

Day et al. 1987; Perez-Hernandez et al. 2002; Stewart et al. 1993a; Stewart et al. 1993b; Špinka et al. 1992) for our research it is per one session. The last important characteristic is which animal initiated and terminated the suckling bout. The initiation of suckling by the foal means that the foal goes simultaneously to the mare and starts suckling. Occasionally, it can happen that the suckling bout is initiated by the mare. It is the situation when the foal is e.g. asleep (lying or standing), mother push the foal by nose and wake him up, and the foal starts suckling. Personally, in my research, I was concerned about the termination and the rejection of suckling bouts. I observed that when the bout was terminated by mare (walking away, kick, bite, moving the tail), or the foal ended the bout itself, or was ended by other herd mate, or disturbance by people. I recorded other data which could affect suckling behaviour like the position (The most common position during suckling among equids is anti-parallel [reverse-parallel position], sometimes can occur parallel [perpendicular position], or behind position), the side of the mare (left, right, behind), activity of the mare and the foal (before, during and after suckling bout), the position of ears during suckling bout, the type of the place (stable, yard, enclosure) and weather.

2.2. Three zebra species

The thesis is based on research of three zebra species. Zebra species look very similar on the first sight, but from morphological and ethological point of view they are very different. The genus *Equus* is the only one genus of equidae (Groves & Bell 2004) and scientist are united that it is monophyletic (Orlando et al. 2009; Price & Bininda-Emonds 2009; Steiner & Ryder 2011). However, phylogeny shows us different evolutionary development of these species among euqids. Several studies have been done about evolution of equids recently (Groves et al. 2004; Oakenfull & Clegg 1998; Oakenfull et al. 2000; Orlando et al. 2009; Piras et al. 2009; Price & Bininda-Emonds 2009; Steiner & Ryder 2011) and in the past, too (Bennet 1980; Eisnmann 1980; Flint et al. 1990; George & Ryder 1986; Harris & Porter 1980; Kaminski 1979; Lowenstein & Ryder 1985; Ryder et al. 1978, Ryder et al. 1979). The studies support each other in many ways, but in some points the researchers came to completely different conclusions than the others. The most often published result about zebra is that this group of equids (plains zebra, Grevy’s zebra and mountain zebra) is monophyletic (George & Ryder 1986; Harris & Porter 1980; Kaminski 1979; Lowenstein & Ryder 1985; Oakenfull & Clegg 1998; Oakenfull et al. 2000; Ryder et al. 1978, Ryder et al. 1979; Steiner & Ryder 2011). Nevertheless other studies propose the zebra group as polyphyletic (Bennet 1980; Flint et al. 1990; Orlando et al. 2009; Piras et al. 2009; Price & Bininda-Emonds 2009).

The largest zebra (Grevy’s zebra [*Equus grevyi* Oustalet, 1882]) is weighing around 400kg (Ginsberg 1988; Rząśnicki 1951). It has extremely fluid social organization (Klingel 1974). Females stay in groups, which consist of approximetly 10 mares and their latest 1 or 2 foals. Groups are without fix membership and hierarchy, long-time bonds are just between mares and foals (Ginsberg 1988; Klingel 1974). On the contrary males are territorial. They defend their territories, which is about 2 to 11 square kilometres large (Ginsberg, 1988; Klingel 1974). Reproduction take place on these territories, so females usually bred with several males, according to their move across the territories (Ginsberg 1988; Klingel 1974). Gestation period varies between 387-482 days (Iaderosa 1983). The distribution of Grevy’s zebras is now reduced to northern Kenya (Estes 1991).

Plain zebra (*Equus quagga* Boddaert, 1785, formerly *Equus burchelli*), on contrary to monotypic Grevy’s zebra (Groves et al. 2004), have six subspecies (Wilson & Reeder 2005; Groves et al. 2004). The subspecies of plains zebra are: Extinct Quagga (*Equus* *quagga quagga* Boddaert, 1785), Burchell's zebra (*Equus quagga burchellii* Gray, 1824), Chapman's zebra (*Equus quagga chapmani* Layard, 1865), Grant's zebra (*Equus quagga boehmi* Matschie, 1892), maneless zebra (*Equus quagga borensis* Lönnberg, 1921), Crawshay's zebra (*Equus quagga crawshayi* De Winton, 1896). My study is based on research of the following three subspecies of plains zebra (Chapman's zebra, Grant's zebra and maneless zebra). Distribution of the plains zebra is larger than the distribution of two other zebra species. The distribution spreads from Somali-Masai Arid Zone through the Southern Savanna and peripherally in the South West Arid Zone, from southern Sudan to South Africa and Angola (Kingdon 1979; Rau 1983). All plains zebras are smaller (127–140cm) than Grevy’s zebra (Grubb 1981; Kingdon 1979) which weights around 175 to 385kg (Grubb 1981; Kingdon 1979). It is one of the most adaptable and successful grazer (Bell 1971). It lives in fixed social groups called harems with one stallion which usually only reproduce. Groups consist of 5 – 6 monandrous females, and maximum herd size is 15 animals (Klingel 1967; Smuts 1976). Harem is not usually territorial but migratory (Ginsberg et al. 1989; Klingel 1967). Gestation period of mares is approximately 360 days (King 1965; Wackernagel 1964). Young males form so called bachelor herds, average size of the bachelor herd is 3-6 individuals (Klingel 1967).

The last living zebra species is mountain zebra (*Equus zebra* Linnaeus, 1758) which consists of two subspecies (Cape mountain zebra [*Equus zebra zebra* Linnaeus, 1758] and Hartmann's mountain zebra [*Equus zebra hartmannae* Matschie, 1898]), but Groves & Bell (2004) suggested that they should be two separate species. Distribution of the species was formerly widespread in the arid mountain ranges parallel the coast from southern Angola to the Transvaal. Hartmann’s zebras inhabit the mountains bordering Namib Desert now days (Smithers 1983). Hartmann’s zebra are 150cm large with average of 298kg weight (Smithers 1983). These equids form harems like plains zebra however, slightly smaller groups (2 – 8 individuals) (Klingel 1968; Penzhorn 1984) and bachelor herds consist of young males and occasionally yearling females, or older stallions that have lost their harems (Smithers 1983). Hartmann’s zebra mares are really intolerant to their yearlings before and after next foaling, yearlings must leave the group (Joubert 1972a). Mountain zebra has got gestation period 362 – 375 days long (Joubert 1972a, b; Penzhorn 1984).

All three zebra species foals are so called followers. Their young stand up early after parturition and follow their mothers for the most of the time before weaning (Lent 1974; Leuthold 1977; Thompson 1996). A little different about this are Grevy’s zebras, because their foals sometimes forms groups that are called “kindergartens” (Klingel 1974), this has never been seen among other zebra species.

How I was able to determine individuals within the group of zebras? I learned the specific patterns of all individuals from observed herds. Each individual has its own card in the ZOO with photos of both sides of the body. The documents were provided to me by curator before and during research. The most suitable places to check differences in stripes pattern for recognition of Grevy’s zebra individuals is recommended to look at the rump. The plains zebra’s marks are visible the best at the whole body due to wider stripes. The mountain zebra’s recognition marks are usually best visible on the shoulder.

2.3. What is known about allonursing?

Allonursing is an act when mammal female nurses offspring(s) that are not her own (Lewandrowski et al. 1983; Roulin 2002). Packer et al. (1992) summarized allonursing among many mammalian species (bats, monkeys, lemurs, wolfs, lions, seals, bison, cattle, elephants, horses, gazelles...). The event has been rarely reported among monotocous species as e.g. perissodactylas (Cameron et al. 1999a; Lloyd & Harper 1980; Penzhorn 1984; Pluháček et al. 2011). There have been a few records of allonursing among perissodactylas. For instance the foal (*Equus caballus* Linnaeus, 1758) was observed to try to be allonursed, but it wasn’t successful said Crowell-Davis (1985). Allonursing has never been recorded in connection with domestic horses among unrelated individuals (Crowell-Davis 1985; Tyler 1972), at one study they observed allonursing among feral horses on New Zealand, which was the case of kin adoption (Cameron et al. 1999a). I know just about three other studies which show allonursing among equids (Lloyd & Harper 1980; Penzhorn 1984; Pluháček et al. 2011). All of these researches consider allonursing as extremely rare event among their species. Packer et al. (1992) discovered that allonursing is more frequent in captive than in wildlife populations.

Nonetheless, the function of allonursing for female is still questionable in wildlife as in captivity. Roulin (2002) has summarized all known hypotheses explaining why allonursing happens among some species: The misdirected parental care hypothesis, the reciprocity hypothesis, the kin selection hypothesis, the milk evacuation hypothesis, the parenting hypothesis. The misdirected parental care hypothesis predicts that mother transfers milk to alien offspring inadvertently, because the allosuckler is stealing her milk (Cameron et al. 1999a; Packer et al. 1992; Roulin 2002). It can collocate with sizes of litter, as in crowded families it can be more difficult to find out the thief (Packer et al. 1992).

The reciprocity hypothesis proposes that females which allonurse mutually their offspring achieve higher fitness (Pusey & Packer 1994). The kin selection hypothesis suggests that mother nurse alien offspring just if they have communal genes to increase her inclusive fitness (Packer et al. 1992). However, if the social group consists of related and unrelated females they need to recognize who is related and who is not (Pusey & Packer 1994).

The milk evacuation hypothesis says that mother provide to alien offspring milk which her own offspring did not drink (Wilkinson 1992). The parenting hypothesis proposes that it is situation if an inexperienced female nurse alien offspring to enhance their maternal skills (Roulin 2002). I took in account all of these proposed hypotheses, and I discussed them.

What are the advantages and disadvantages of allosuckling for young? Allosuckers can gain extra energy (Packer et al. 1992), this is commonly accepted. However, Víchová & Bartoš (2005) didn’t find any significant profit in condition of allosuckers at cows. Roulin & Heeb (1999) suggested that allosuckling young can have immunological advantage, and improve their resistance against pathogens and parasites. On the other hand pathogen transmission can be disadvantage for allosuckers, too (Kreis 1997; Vochem et al. 1998).

3. THE FIRST MANUSCRIPT

3.1. Title

Effect of social organization and ecological adaptation on mother-infant behaviour in three zebra species

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3.3. Abstract

The three extant zebra species differ in their ecology and social system. In the wild, mountain (*Equus zebra*) and Grevy's zebra (*Equus grevyi*) live in an arid environment while plains zebra (*Equus burchellii*) inhabit savannah. Mountain and plains zebra mares form stable herds associated with high aggression and low aggression, respectively. Grevy's zebra females form loose associations with the lowest level of aggression. While rejection and termination of suckling bouts can reflect maternal investment, suckling bout duration and frequency may express intensity of maternal care. The aim of this study was to re-evaluate the suggestion of previous studies that suckling bout duration and frequency are influenced by environmental adaptations in equids. 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 lower rate of mother's rejection and termination of suckling bouts by the mother than plains zebra. Therefore mothers of species that evolved in more arid habitat were more tolerant towards their offspring than those of species evolved in mesic habitat. On the other hand, suckling bout duration was longest and most frequent in mountain zebra, followed by plains and Grevy's zebra. This result coincides with the rate of aggression among mares; foals spent more time by suckling in species where more aggression occurred. Thus, while termination and rejection seems to be affected by ecological adaptation, suckling bout duration and frequency reflects social needs of the foal.

Key words: *Equus*, suckling behaviour, zebra, social system, ecological adaptation, parental care

3.4. Introduction

"The key to sociobiology of mammals is milk" (Wilson 1975). Lactation is a far more demanding form of maternal investment than gestation, oestrus 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 burchellii*: Fischhoff et al. 2007) and Grevy's zebra (*Equus grevyi*: Sundaresan et al. 2007b), feral horses (*Equus caballus*: Rubenstein 1993) as well as in other ungulates (e.g. 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 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; Ralls et al. 1987; Andersen 1992). Therefore zebras are particularly valuable 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 a few studies compare the suckling behaviour of several species (e.g. Trillmich 1990; Lavigueur & Barrette 1992; Maestripieri 1994a). The only interspecific comparison of equid suckling behaviour was published from wild Grevy's and plains zebra (Becker & Ginsberg 1990) comparing also data from the literature on feral horses (Tyler 1972; Crowell-Davis 1985). Becker and Ginsberg (1990) concluded that Grevy's zebra foals spent the least amount of time suckling and had the longest intervals between suckling bouts compared to other equids. Therefore they proposed that the accelerated foal development in Grevy's zebra compared to other equids would be an adaptation to arid environment (Becker & Ginsberg 1990).

However, ten years later a meta-analysis of studies in mammals that 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). Moreover, in feral horses (Cameron 1999 et al.), fallow deer (*Dama dama*: Birgersson & Ekvall 1994), domestic mice (*Mus domesticus*: Mendl & Paul 1989) and domestic cats (*Felis cattus*: Mendl and Paul 1989), no significant relationship between suckling bout duration and/or suckling frequency and milk or energy intake was found. 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; Cameron & Linklater 2000; Cameron et al. 2003). Nevertheless, Becker and Ginsberg (1990) did not include rejection and termination of suckling bouts in their analyses. It should be also noted that, although suckling bout duration and suckling frequency could not be used as an indicator of milk transfer, but these behavioural measurements of nursing are useful to assess the amount of maternal care in current offspring (Mendl & Paul 1989; Cassinello 2001; Cameron et al. 2003; Therrien et al. 2007).

Besides the study by (Becker & Ginsberg 1990), the reports of suckling behaviour in mountain and Grevy’s zebra are very rare, and in these few cases there were 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 1983b; Dwyer & Lawrence 2000; Dwyer et al. 2001). If these differences are of genetic origin they should be detectable and persist in captivity. Therefore, the main aim of this study is to re-evaluate the suggestions made by Becker and Ginsberg (1990) that suckling behaviour reflects adaptation to the habitat quality where the species evolved using rejection and termination of suckling bouts in three captive zebra species kept in the same facility (thus under same living conditions).

3.5. Methods

3.5.1. Animals

We observed 43 foals (29 plains zebra, 8 Grevy’s zebra, and 6 mountain zebra) in five different herds (three of them being plains zebra) at the Dvůr Králové Zoo, Czech Republic (see Table 1). The herd sizes ranged from two to 14 breeding mares, aged from four 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) and mammals in general (Green et al. 1993; Bateson 1994), we excluded foals (13 plains zebra) of pregnant mares from all the analyses.

In the summer all herds were in an enclosure (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, and therefore they were 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* the whole time. Food including also pellets and carrot was given fresh daily, usually in the morning. As in our previous study, the dominance hierarchy among the adult females was based on observed biting and offensive kicking (Pluháček et al. 2006). Comparing the dyadic interactions between mares we expressed rank by a simple criterion of the number of mares which dominated the focal individual (further referred to as “number of dominant mares”).

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 08h00 to 11h00 or from 14h00 to 17h00 on Saturday or Sunday. This timing reflected peaks of suckling activity found in wild and feral equid populations (Joubert 1972a). For detailed observation methods see (Pluháček et al. 2007). In total, we carried out 1626 hours of observation (542 sessions over 358 days). The respective herds were observed for 549 (herd 1 of plains zebra), 489 (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. 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 Pluháček et al. 2010a, b, c). 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.

3.5.2. Statistics

All data were analyzed using the SAS System, Version 9.2. Factors influencing the suckling bout duration and frequency were tested using a multivariate general linear mixed model (GLMM, PROC MIXED, SAS). 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 GENMOD procedure (SAS). We tested the probability that (i) the suckling bout was successful (i.e. not rejected by the mother within five seconds), and (ii) the mother terminated the suckling bout. Fixed factors (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, 2008/2010), the mother’s age, 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), and the feeding state of the mother (“yes”, “no”, “interrupted due to nursing”), 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. We started with the full model including all of the fixed effects and sequentially dropped those effects which were not significant. Since this was an unbalanced design, with more than one effect, the arithmetic mean for a group did not accurately reflect the response for that group, because it did not take into account the other effects. Thus, the within-group means were appropriately adjusted for the other effects in the model (LSMEANs statement). The differences between the means were tested by *t* – test with multiple comparisons we used the Tukey–Kramer adjustment.

3.6. *Results*

In total, we recorded 4626 successful suckling bouts and 2763 unsuccessful suckling attempts rejected by the mare. For respective species (plains zebra, Grevy's zebra, and mountain zebra) we recorded 2193, 1705, and 842 successful suckling bouts and 1687, 825, and 295 unsuccessful suckling attempts rejected by the mare.

3.6.1. Rejection of suckling attempts

The logistic regression model showed that the interaction between age of the foal and species ($\chi^2_2 = 7.47$, $P = 0.024$; Fig. 1) was related to the probability of successful suckling. Plains zebra mares refused more solicitations by the foal (44 %, $N = 3712$) than Grevy's zebra (33 %, $N = 2530$, $\chi^2_1 = 15.49$, $P < 0.0001$) or mountain zebra (26 %, $N = 1137$, $\chi^2_1 = 30.42$, $P < 0.0001$). Mares of Grevy's zebra tended to reject more suckling solicitations of the foal than mountain zebra mares ($\chi^2_1 = 3.32$, $P = 0.068$). The probability of successful suckling did not change in plains or mountain zebra, but it increased with increasing age of the foal in Grevy's zebra ($Z = 2.99$, $P = 0.0028$). The last factor affecting the probability of successful suckling was feeding status of the mother ($\chi^2_1 = 11.75$, $P = 0.0006$). 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 %, $N = 4885$).

3.6.2. Suckling bout duration

The duration of suckling bouts decreased with increasing age of the foal ($F_{1.4508} = 149.76$, $P < 0.0001$). Duration was affected by the animal who terminated the bout ($F_{2.4508} = 180.84$, $P < 0.0001$), by the interaction between species and the animal who terminated the bout ($F_{4.4508} = 21.71$, $P < 0.0001$), and by the feeding status of the mare at the beginning of the suckling bout ($F_{2.4508} = 33.16$, $P < 0.0001$),

In all three zebra species suckling bouts terminated by the foal were longer than those terminated by the mare (plains z.: $t_{4508} = 7.97$, $P < 0.0001$; Grevy's z. $t_{4508} = 6.88$, $P < 0.0001$; mountain z.: $t_{4508} = 14.83$, $P < 0.0001$) or by a herdmate (plains z.: $t_{4508} = 5.81$, $P < 0.0001$; Grevy's z.: $t_{4508} = 2.59$, $P = 0.0089$; mountain z.: $t_{4508} = 6.28$, $P < 0.0001$). The suckling bouts were shorter when terminated by a herdmate than when terminated by the mare in plains zebra only ($t_{4508} = 3.49$, $P = 0.0146$).

For the next step, we ran three separate analyses for suckling bout duration in bouts terminated by the foal, the mare, and by a herdmate. When terminated by a herdmate, the suckling bout duration did not differ among species ($F_{2.53} = 0.60$, NS); when terminated by the mare, suckling bout duration did differ among species ($F_{2.1162} = 3.26$, $P = 0.0338$): suckling bout duration was shorter in Grevy's zebra than in plains zebra ($t_{1162} = 2.65$, $P < 0.0110$; Fig. 2). The suckling bout duration terminated by a mountain zebra mare did not differ from that of the other species (Fig. 2). When terminated by a foal, again the suckling bout duration differed among species ($F_{2.3239} = 19.04$, $P < 0.0001$). The suckling bout duration was longer in mountain zebra than in plains ($t_{3239} = 4.87$, $P < 0.0001$) or Grevy's zebra ($t_{3239} = 6.03$, $P < 0.0001$) and it was longer in plains zebra than in Grevy's zebra ($t_{3239} = 1.95$, $P = 0.0490$; Fig. 2).

3.6.3. *Suckling bout frequency and total time spent by suckling*

Suckling bout frequency has been affected by the age of the foal ($F_{1.1148} = 548.45$, $P < 0.0001$), by the species ($F_{1.1148} = 6.80$, $P = 0.0012$) and by the interaction between the age of the foal and the species ($F_{1.1148} = 11.13$, $P < 0.0001$). The highest suckling bout frequency has been observed in plains zebra followed by that of mountain zebra and the lowest suckling frequency has been recorded in Grevy's zebra (Fig. 3). Similarly, the total time spent suckling during one observation period was affected by the age of the foal ($F_{1.1148} = 671.80$, $P < 0.0001$), by the species ($F_{1.1148} = 7.17$, $P = 0.0008$) and by the interaction between the age of the foal and the species ($F_{1.1148} = 10.07$, $P < 0.0001$). Again, the shortest time spent suckling was recorded in Grevy's zebra, but we did not find any difference between plains and mountain zebra (Fig. 4).

3.6.4. *Suckling bout termination*

The probability of suckling bouts being terminated by the mother was affected by the foal's age ($\chi^2_1 = 11.88$, $P = 0.0006$), the interaction between the foal's age and species ($\chi^2_2 = 6.93$, $P = 0.0312$; Figure 5), and the feeding status of the mother at the start of the suckling bout ($\chi^2_1 = 8.78$, $P = 0.0030$). 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, $\chi^2_1 = 13.77$, $P = 0.0002$) and mountain zebra (24.9 %, $N = 820$ bouts, $\chi^2_1 = 3.93$, $P = 0.0474$). Mountain zebra mothers terminated more suckling bouts than Grevy's zebra mothers ($\chi^2_1 = 5.51$, $P = 0.0189$). When the mother was feeding while nursing the proportion of suckling bouts terminated by her was lower than when she was not feeding.

According to our analysis of GEE parameter estimates, in plains zebra foals, the proportion of suckling bouts terminated by the mother decreased with increasing age of the foal ($Z = 2.15$, $P = 0.0317$) while in Grevy's and mountain zebra the proportion of suckling bouts terminated by the mother was not affected by the age of the foal (Fig. 5).

3.6.5. Rate of agonistic interactions

In total we recorded 2312 agonistic interactions among adult mares. The rate of agonistic interactions per individual during one hour of observation was highest in mountain zebra (0.90), lower in plains zebra (0.52) and the lowest in Grevy's zebra (0.09).

3.7. Discussion

We found that mothers of both species originating from an arid environment (mountain and Grevy's zebras) rejected and terminated lower rate of suckling bouts/attempts than those of plains zebra inhabiting 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 more 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). Therefore, mothers of the species which evolved in an arid environment perhaps compensate more the demands of their foals because other resources available for the foals are more limited than in the species evolved in mesic environment. It seems that this result is somewhat in contradiction to parent-offspring conflict theory (Trivers 1974) suggesting higher conflict when resources are scarce (Festa-Bianchet 1988). It should be noted, however, that the mares we observed were not pregnant the level of conflict was low. Likewise, the reason for an increased tolerance could be good living conditions with higher availability of food and water provided in the zoo.

On the other hand, suckling bout duration was the longest and most frequent in mountain zebra, followed by plains and Grevy's zebra. Thus, suckling bout duration does not necessarily reflect evolutionary adaptation to an arid environment. It should be noted that 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; Therrien et al. 2007; Pluháček et al. 2010a). Our results suggested that suckling bout duration increased with intraspecific aggression rate among adult females of the species. A similar effect of relationships among adults on maternal style was recorded in interspecific comparisons of several macaque species (Kaufman & Rosenblum 1969; Thierry 1985; Maestripieri 1994a, b). Therefore, while termination and rejection seems to be affected by ecological adaptation, suckling bout duration and the time spent suckling can reflect social needs of the foal. This has been given as a possible explanation for high suckling frequency in studies on white-tailed deer

(*Odocoileus virginianus*) and fallow deer (*Dama dama*: Lavigueur & Barrette 1992; Therrien et al. 2007). In primates suckling duration is correlated with stress reduction (Gomendio 1990; Clutton-Brock 1991; Redondo et al. 1992), and in cattle (*Bos taurus*) with socialization with the dam (Das et al. 2000). Since 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 zebra in particular.

The other explanation consistent with our results is that suckling bout duration reflects phylogeny of zebras. According to almost all studies, the mountain zebra separated earlier than plains and Grevy's zebras (George & Ryder 1986; Oakenfull et al. 2000; Leonard et al. 2005; but see Oakenfull & Clegg 1998). The longest suckling bout duration found in mountain zebra could be an apomorphic trait within the zebra lineage. This could be supported by the fact that differences in suckling behaviour exist between breeds of horses, cattle and sheep (*Ovis aries*) and it is possible that these differences are of genetic origin (Carson & Wood-Gush 1983b; Das et al. 2000; Dwyer & Lawrence 2000; Dwyer et al. 2001). Although some studies on horses and feral asses found the same suckling bout duration as we recorded for mountain zebra in our study (Carson & Wood-Gush 1983a; Barber & Crowell-Davis 1994; Moehlman 1998; Cameron et al. 1999), most researchers reported that it suckling bout duration and frequency of horses and asses are similar to those we found in plains and Grevy's zebra (Tyler 1972; Rogalski 1973; Schoen et al. 1976; Crowell-Davis 1985; Rutberg 1990; Smith-Funk & Crowell-Davis 1992; Heitor & Vicente 2008). It should be noted that while feral horses are highly variable in social life, the zebras are very conservative (Berger 1988).

Although maternal care depends on environmental conditions (Bateson 1994), recent experiments in captive rhesus macaques (*Macaca mulatta*) 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. Since all the zebras lived in identical climatic environment (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 different environment in the three species studied here.

Equid milk has a low energy content, which implies that mares must produce a large volume of milk to supply the energy needs of the 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; Schryver et al. 1986; Oftedal & Jenness 1988). Therefore, milk composition probably cannot explain the differences in suckling behaviour of the three zebra species.

Our results dealing with suckling bout duration and frequency are a little different from those of Becker and Ginsberg (1990). In both studies the lowest suckling frequency and time spent suckling was observed in Grevy’s zebra. However, contrasting with the results of Becker and Ginsberg (1990) we recorded longer suckling bout duration in plains than in Grevy’s zebra. In our earlier study on captive plains zebra 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. 2010a); 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 and 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 offers the first detailed report of suckling behaviour in mountain zebra. Mountain zebras in the present study had the longest suckling bout duration 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 1972a, b; Penzhorn 1984a), which are among the highest values reported for equids (Waring 2003). On the other hand we did not record any interruption 10 seconds before the end of the bout as reported from the wild (Joubert 1972a, b; Penzhorn 1984a). The higher suckling frequency recorded in our study compared to other studies (Joubert 1972b; Penzhorn 1984a) could be explained by captive conditions including water availability.

We can conclude that mother-offspring conflict (in terms of rejection and termination of suckling bouts) was lower in species adapted to arid environment than in a less arid-adapted species. Since suckling bout duration increased with increasing aggression rate among mares of the species, the results of our study support the hypothesis that suckling bout duration reflects social needs of the foal rather than milk intake requirements.

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3.9. *Tables*

Tabel 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. burchellii*	F	1 / 1999	36	113
Pelopones	Pinta	*E. burchellii*	M	1 / 1999	0	330
Paris	Palmyra	*E. burchellii*	M	1 / 2001	96	278
Ptolemaios	Piki	*E. burchellii*	M	1 / 2001	94	276
Paula	Palmyra	*E. burchellii*	F	1 / 2008	4	432
Rubi	Karma	*E. burchellii*	F	1 / 2008	2	261
Irwin	Irkasa	*E. burchellii*	M	1 / 2008	4	298
Linda	Karolína	*E. burchellii*	F	1 / 2008	4	173
Masud	Meri	*E. burchellii*	M	2 / 1999	3	143
Delos	Duky	*E. burchellii*	M	2 / 1999	0	84
Akin	Alžběta	*E. burchellii*	M	2 / 2008	100	394
Padme	Penta	*E. burchellii*	F	2 / 2008	26	320
Kid	Kity	*E. burchellii*	M	3 / 1999	1	245
Beata	Boma	*E. burchellii*	F	3 / 1999	4	75
Accra	Angelika	*E. burchellii*	F	3 / 2001	3	101
Kikwit	Katrin	*E. burchellii*	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

3.10. Figures

Figure 1. The probability of successful suckling according to the age of foal and the species.

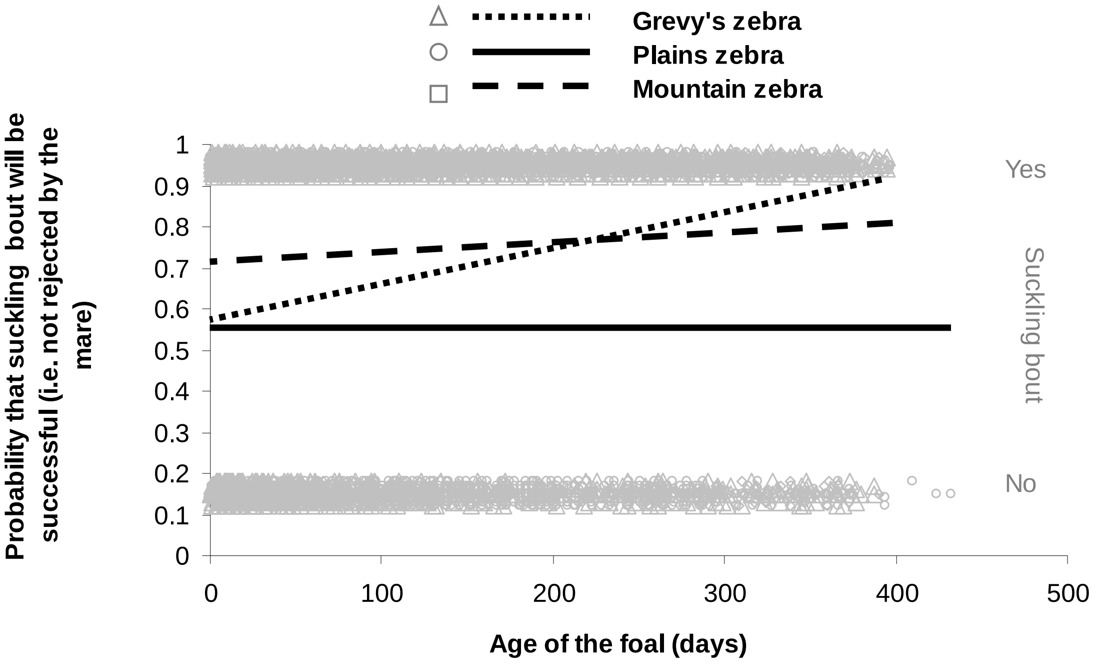


Figure 2. The suckling bout duration in three zebra species according to the animal terminating the bout and the identity of species (mean ± SE). Only significant differences between species are shown.

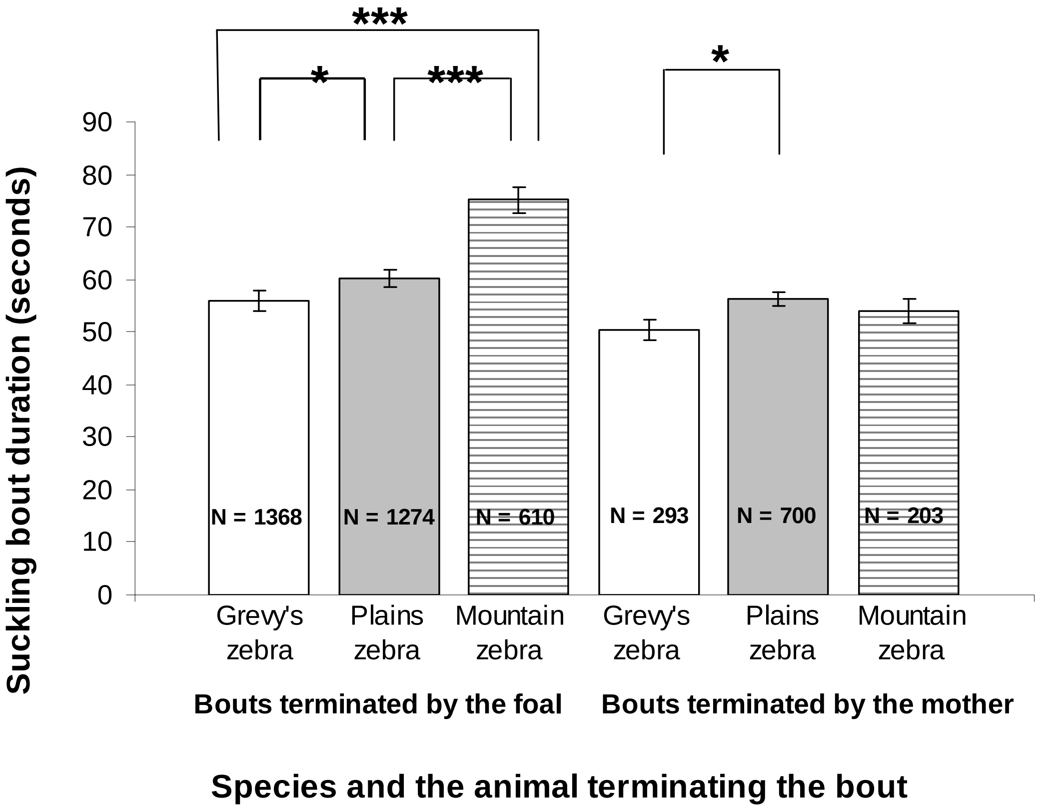


Figure 3. The frequency of suckling bouts within the 180 minutes observation session according to the age of foal and the species.

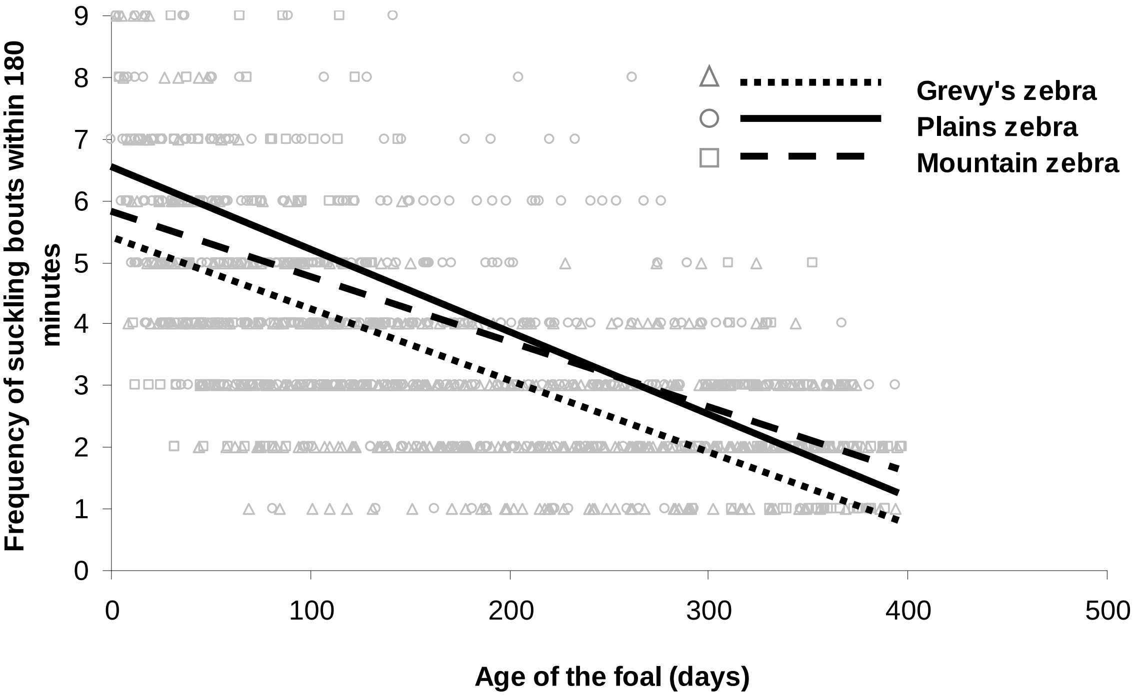


Figure 4. The total time spent by suckling within the 180 minutes observation session according to the species.

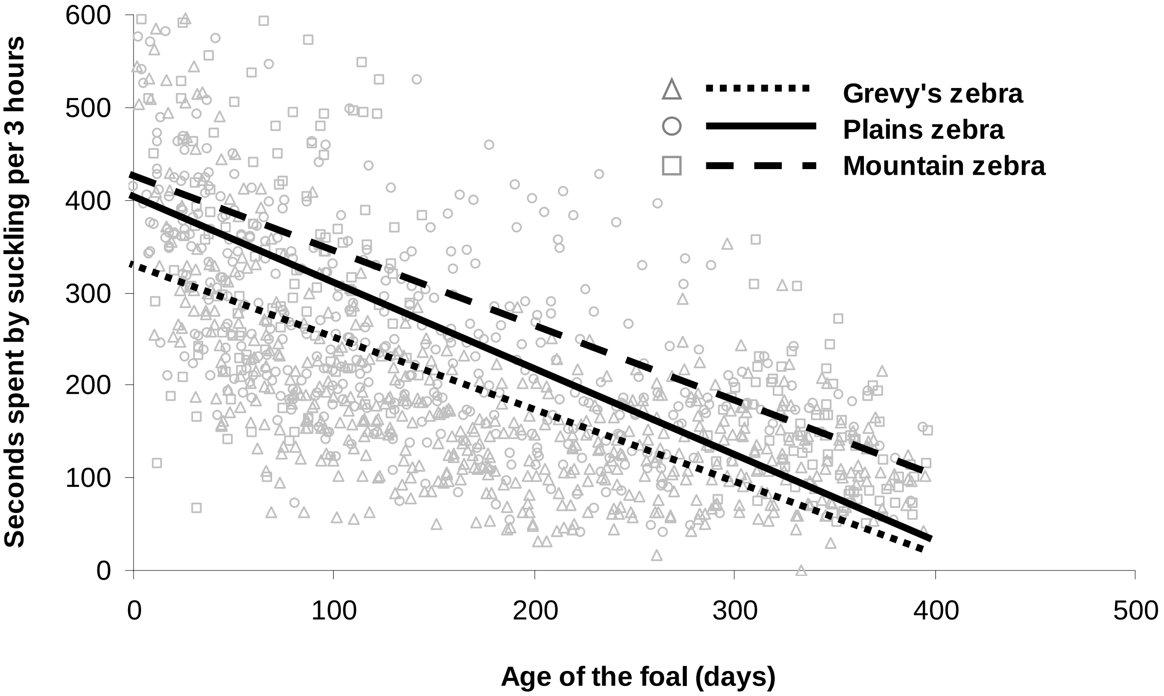
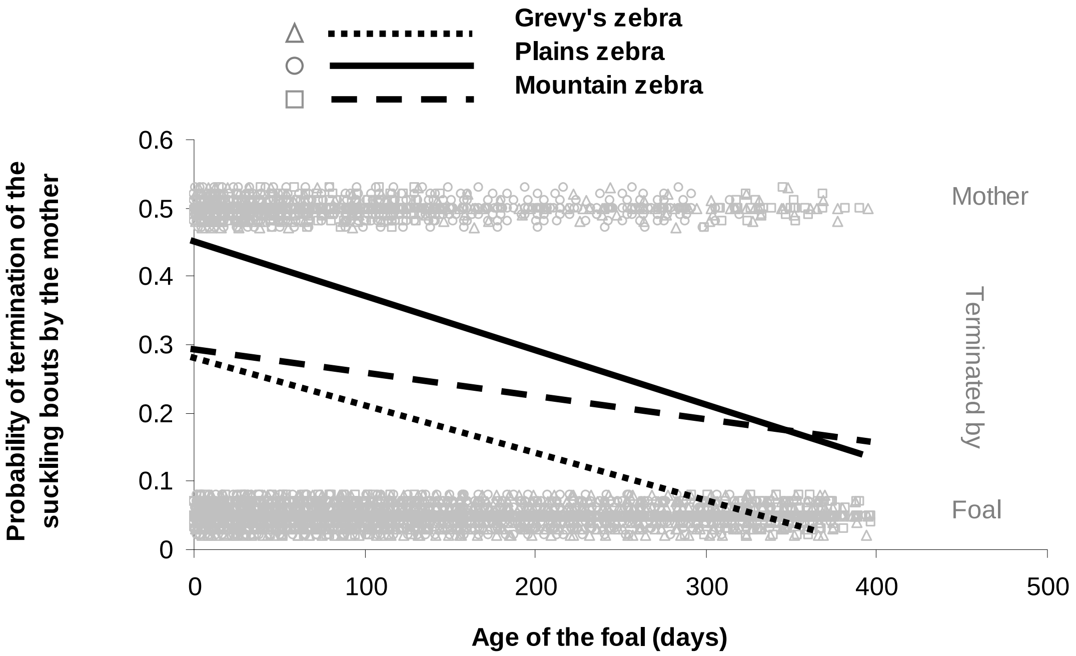


Figure 5. The probability of suckling bouts terminated by the mother according to the age of foal and the species.



4. THE SECOND MANUSCRIPT

4.1. *Title*

Effect of social system on allosuckling and adoption in zebras

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4.3. Abstract

Although nursing non-filial offspring (allonursing) represents costly behaviour to the female, it occurs in a variety of taxa, including ungulates. The three only existing species zebra species differ in their ecology and social system. In the wild, mountain and Grevy's zebra live in arid environments while plains zebra 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 hours 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. If a Grevy's zebra mare allowed occasional allosuckling by a non-fillial foal, the probability of long-term allosuckling was smaller than 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.

Key words:

Equus, allonursing, mother-infant behaviour, zoo, adoption, Grevy's zebra

4.4. 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 & Pusey 1992).

Among ungulates, allonursing occurs in artiodactyls (water buffalo, *Bubalus bubalus*: 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 et al. 2009b), but is rare in equids. All reported cases of allonursing in equids (two 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; one in feral horses *Equus ferus caballus*: Cameron et al. 1999a) involved individual adoption of non-filial foal only. Excluding adoption, 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 and Ginsberg 1990), who found that Grevy’s zebra 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 (*Equus 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 arid (guanaco; Dromedary camel *Camelus dromedarius*: Gauthier-Pilters & Dagg 1981; Saharan arrui *Ammotragus lervia*: Cassinello 1999) as well as mesic (waterbuck, *Kobus defassa*: Spinage 1969; fallow deer *Dama dama*: Ekvall 1998) environment. On the other hand the occurrence of allonursing may be influenced by social structure as reported for red and fallow deer (Ekvall, 1998; Landete-Castillejos et al. 2000). Whereas in populations forming socially stable herds allonursing takes place frequently it has not been recorded in populations of unstable group structure (Ekvall, 1998). Most other 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. We focused if allonursing in zebras could be explained by differences in social structure or by different environment 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.

4.5. Materials and Methods

4.5.1. Animals

We observed three zebra species (29 foals and 23 mares of plains zebra in three herds, eight foals and 18 mares of Grevy’s zebra in one herd, and six foals and nine 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 Dvůr Králové zoo and the social history of all three species did not differ, excluding individual housing of mountain zebra (see later). 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 hours 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 places (at least two) were in each enclosure or stable, therefore animals did not need to visit the same feeding station.

Plains zebras were observed from January 1999 to March 2002. All three species were observed from September 2008 to July 2010. Two observers (MO, JP) performed the observations in four different sessions each week using the same methods as (Pluháček et al. 2007; 2010a,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 behavior of equids (Becker & Ginsberg 1990; Cameron et al. 1999b). A suckling bout was regarded as successful when it lasted longer than five 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 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 seconds).

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, etc.) 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 08h00 to 11h00 or 14h00 to 17h00 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 hours of observation (542 sessions over 358 days). The respective herds were observed for 549 hours (plains zebra herd 1), 489 hours (plains zebra herd 2), 198 hours (plains zebra herd 3), 270 hours (Grevy’s zebra) and 120 hours (mountain zebra).

4.5.2. Statistics

All data were analysed using the SAS System, Version 9.2. To compare occurrence of allosuckling among the three zebra species we used chi-square and Fisher 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 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 model 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. Since 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 the weaning process of Grevy's zebra starts from 11 month of the age of the foal (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. 1999a; 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. 2010b), 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 model and as subject in the repeated statement in GENMOD models.

4.6. Results

4.6.1. Comparison of allosuckling incidence among three zebra species

In total, we recorded one 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 seven out of 13 cases, the allosuckling occurred simultaneously with suckling by the filial foal. Average success rate was 10%; one foal was not observed to attempt to suckle from any other individual except her mother. 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 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 exact test $P = 0.012$).

4.6.2. Kinship analysis of allonursing in Grevy's zebra

The number of allonursing bouts per mare-foal dyad was affected by kinship ($F = 5.00$; 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).

4.6.3. Position of foal during allosuckling

Most suckling bouts occurred in reverse-parallel position (Grevy's zebra: 91%, n = 1729; plains zebra: 97%, n = 4614; mountain zebra: 93%, n = 295). When unsuccessfully attempted to allosuckle foals were in reverse-parallel position less often (Grevy's zebra: 32%, n = 117; plains zebra: 86%, n = 22; mountain zebra, 100% n = 1). When successfully allosuckled Grevy's zebra foals were in a reverse-parallel, perpendicular to the mare and parallel position in 7, 2 and 4 cases, respectively. Only two (Alf, Kevin) out of five foals allosuckled in a parallel position. Nevertheless, each Grevy's zebra foal attempted to allosuckle from every possible position at least once.

4.6.4. Case report of adoption and allosuckling in Grevy's zebra

The male foal "Kevin" was born to the 21 year old mare "Šárka2" on 1st October 2008. He was her 9th foal. Šárka2 died due to colic when Kevin was six months and two days old. Following her death, he successfully suckled from other nursing mares (Table 2), 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%), where he was refused by the mare. 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 (Table 3).

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 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 ($F = 13.37$; df = 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.

4.7. 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: over 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.

In the wild, Grevy’s zebras inhabit an arid environment (Ginsberg 1989; Bauer et al. 1994). As the 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; Klingel 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; Klingel 1975; Smuts 1976; Penzhorn 1979), Grevy’s zebra females form loose associations which 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 two to three months (Becker & Ginsberg 1990). In this fission-fusion society, if a Grevy’s zebra mare allowed occasional allosuckling by a non-fillial 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 mountain and plains zebra females than for Grevy’s zebra females. It should be noted that difference in social life of zebra females among various species persist when transferred to the captive or semi-captive conditions (Schilder 1992; Berger 1988; Pluháček unpublished data). Also, the social structure of zebras we observed was very similar to that reported in the wild (Klingel 1969; Klingel 1974; Penzhorn 1979). E.g. we have been able to determine social hierarchy in plains and mountain zebra, but no social hierarchy was developed in Grevy’s zebra despite of 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): the kin selection hypothesis , the misdirected parental care, the milk evacuation hypothesis, the reciprocity and parenting (females nurse non-filial offspring to improve their maternal skills) hypothesis and the non-adaptive hypothesis. In contrast to some other studies on allonurisng in ungulates (Lee 1987; Rapaport & Haight 1987; Cameron et al. 1999a; 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. However, our results tentatively seem to support the reciprocal hypothesis since 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. 2009a) or the non-adaptive hypothesis (Hayes 2000) as the possible explanations of allonursing in captive Grevy’s zebra.

On the other hand allonursing is highly beneficial to the young. The milk theft hypothesis is not supported by our data (Landete-Castillejos et al. 2000; Maniscalco et al. 2007; Zapata et al. 2009a, 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, 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 to 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 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 to other foals in the herd, contrasting with the plains zebra case. Apparently, the 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 six 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 five months and 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 a non-filial offspring found in this species.

4.8. References

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4.9. Tables

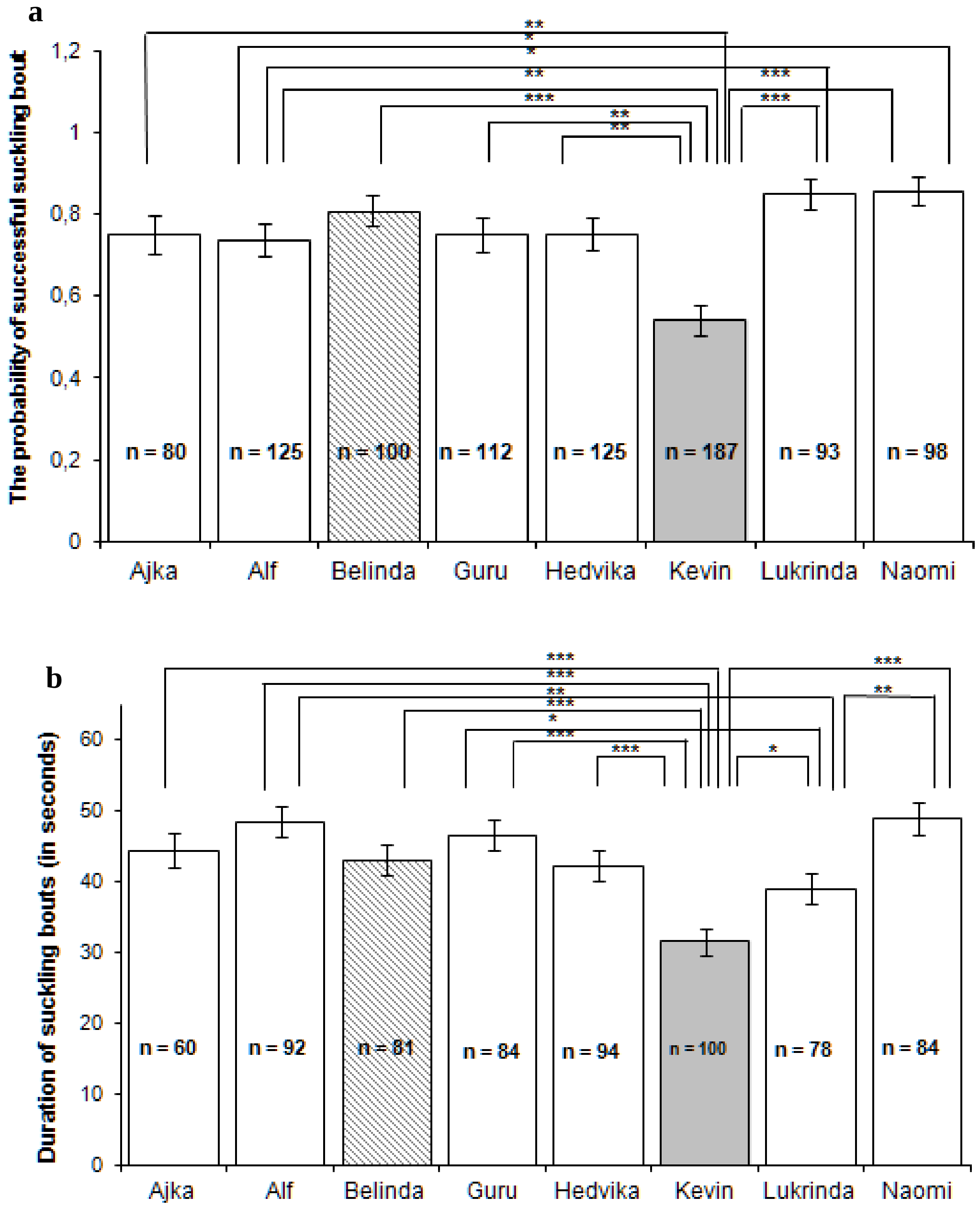
Table 1. Comparison of successful suckling bouts and unsuccessful attempts refused by mother and non-mother among three zebra species. Bouts and attempts by the orphaned foal are excluded.

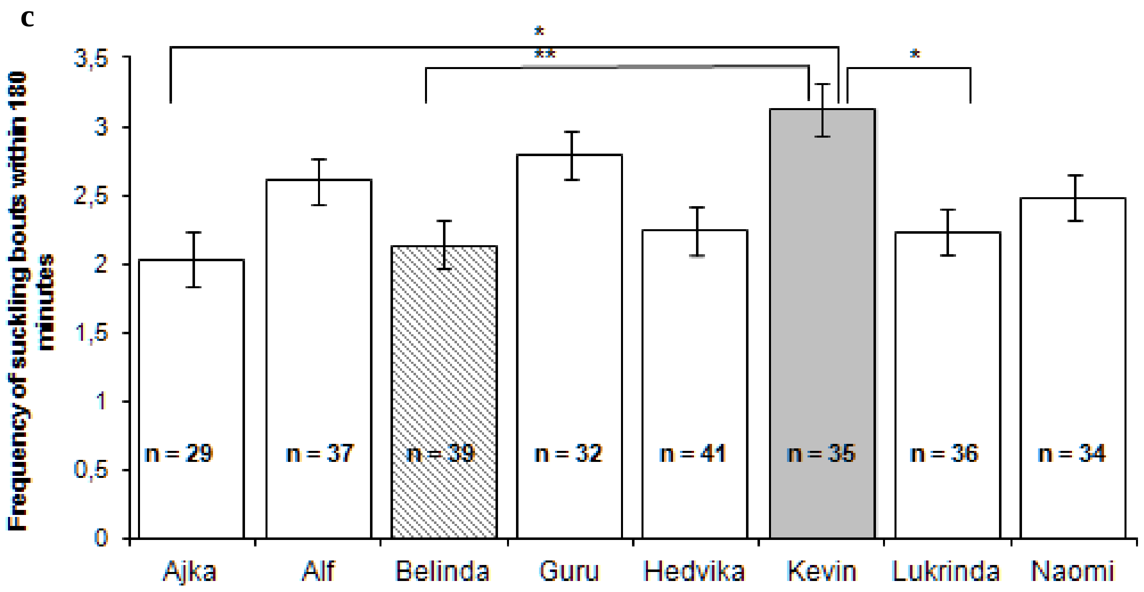
Species	Mother		Non-mother	
	Unsuccessful attempts	Successful suckling bouts	Unsuccessful allosuckling attempts	Successful allosuckling bouts
Grevy’s	824	1729	117	13
Mountain	296	843	1	0
Plains	3192	4614	22	0

4.10. Figures

Figure 1. Nursing and allonursing at the same time in captive Grevy’s zebra at Dvůr Králové Zoo (nursed foal “Guru” is on the left in reverse-parallel position while allonursed foal “Kevin” is on the right in parallel position).

Figure 2. Suckling behaviour of two captive Grevy's zebra foals (filial Belinda and non-filial Kevin) nursed by a mare female (Tabia) compared to control single foals reared in the same herd and season (Ajka, Alf, Guru, Hedvika, Lukrinda, 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 minutes) 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




c
Frequency of suckling bouts within 180 minutes
3,5
3
2,5
2
1,5
1
0,5
0
*
**
*
n = 29
n = 37
n = 39
n = 32
n = 41
n = 35
n = 36
n = 34
Ajka
Alf
Belinda
Guru
Hedvika
Kevin
Lukrinda
Naomi

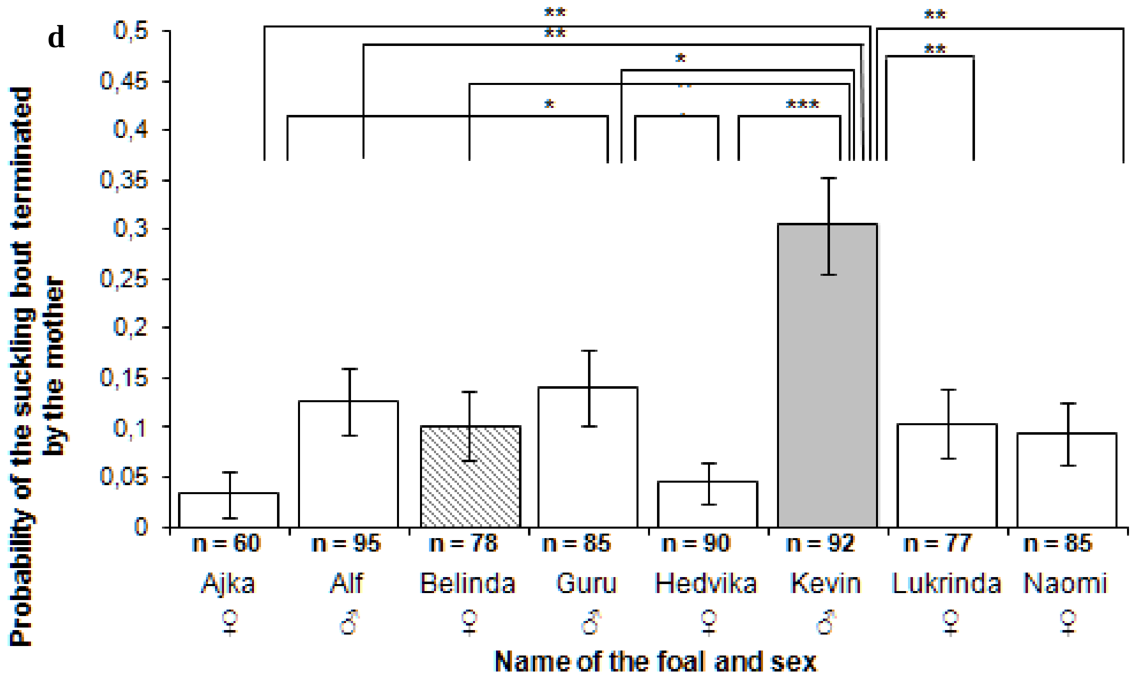
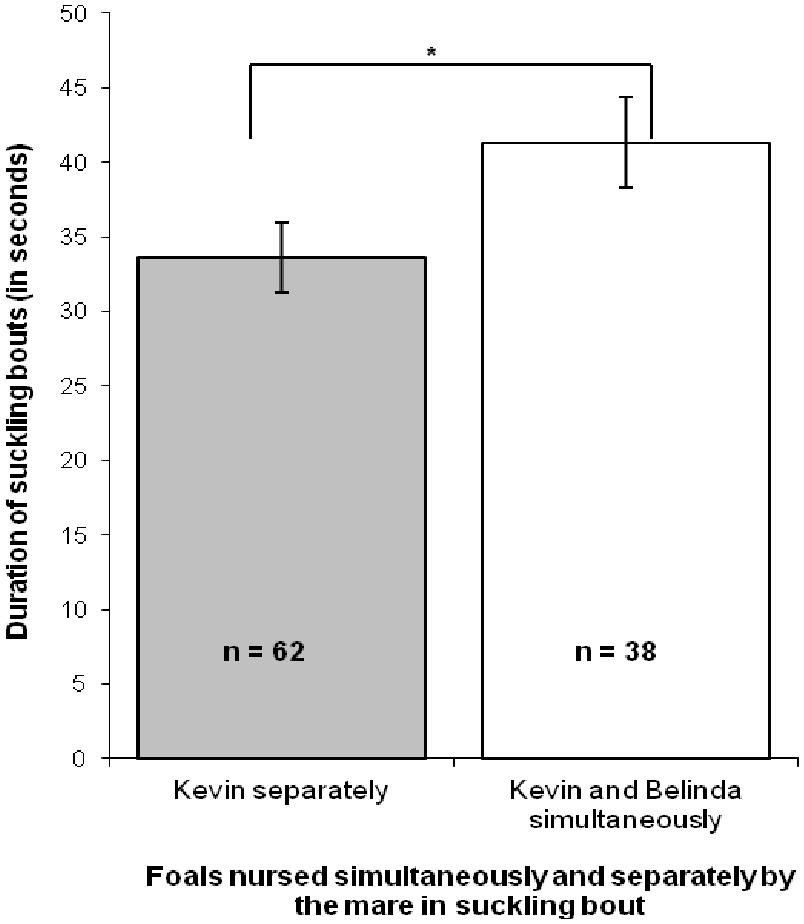

d
Probability of the suckling bout terminated by the mother
0,5
0,45
0,4
0,35
0,3
0,25
0,2
0,15
0,1
0,05
0
**
**
*
*
***
**
**
n = 60
n = 95
n = 78
n = 85
n = 90
n = 92
n = 77
n = 85
Ajka ♀
Alf ♂
Belinda ♀
Guru ♂
Hedvika ♀
Kevin ♂
Lukrinda ♀
Naomi ♀
Name of the foal and sex

Figure 3. Comparison of the duration of suckling bouts by a mare (Tabia) involving one or two foals at the same time (mean ± SE).



5. CONCLUSIONS

The study involves two important aspects of sociobiology and behavioural ecology of zebras: suckling and allosuckling behaviour. I found out that Grevy's and mountain zebra's mothers are more tolerant to foals than the plains zebra's mothers. This finding would be explained by the mother - offspring conflict theory (Trivers 1974). It reflects environmental adaptation of Grevy‘s and mountains zebra better than social differences of female associations. I suppose that foals of arid zebra species need probably more energy to survive in their environment. Mares from an arid environment are willing to invest into the present foals more than zebra from a mezic environment, to reduce probability of death of their descendants. I carried out the first detailed study on suckling behaviour in mountain zebra.

I found out higher tolerance of Grevy‘s zebra mares towards non-filial foals than reported for other zebra species. Allonursing and high incidence of allosuckling attempts in Grevy's zebra are really exceptional events among equids (Berger 1988; Cameron et al. 1999; Crowell-Davis 1985; Lloyd & Harper 1980; Penzhorn 1984; Tyler 1972). I discussed my results in light of five hypotheses explaining allonursing (Roulin 2002). I couldn't support milk theft hypothesis because allosuckling foals performed often used reverse-parallel position, where mares were supposed to determine non-filial foal allosuckling, easily. I also did not find strong support for the kin-selection hypothesis, because incidence of allonursing in Grevy's zebra was affected by kinship, but not by coefficient of relationship. On the other hand, my results seem to be in line with the reciprocal hypothesis because mares are together for along time. Due to the fact that I recorded allonursing by multiparous Grevy's zebra mares, the results are not in line wit the parenting hypothesis. I can't exclude themilk evacuation hypothesis, the misdirected parental care hypothesis or the non-adaptive hypothesis (Hayes 2000) as possible explanations of allonursing in captive Grevy's zebra. In this point I would like to stress that proper research dealing with allonursing among zebras in the wild is missing. Another reason why Grevy's foals attempted to allosuckle so much could be that foal with higher immunity has better condition to survive in more arid environment than that without variable nutrition.

Also I have recorded the first cases of allonursing of orphaned foal by more than two individual mares among equids. Orphaned foal was accepted old enough to survive without milk, and it is very rare among equids. Grevy's zebra mare didn't restrict milk intake to her filial foal as documented in the similar case of plains zebra (Pluháček et al. 2011) where filial foal was nursed less than other plains zebra's foals. If I look on the allonursing hypothesis in this case, it seems to support the misdirected parental care hypothesis (Roulin 2002). However, this hypothesis doesn't explain why Tabia nursed Kevin for so long mainly from perpendicular position, and nursed him also in time when filial foal (Belinda) didn't suckle. Taking in acount the fact that adopted foal was alonursed by the primiparous mare I can not exclude the parenting hypothesis (Roulin 2002).

Allonursing and adoption seem to be connected to social organization of zebra than to environmental adaptation. Packer et al. (1992) imply that allonursing is more common in captivity and they also suggest that it is due to the access to unlimited food. It looks like the reason for an increased tolerance can be good living conditions in captivity. I can't refuse this. Obviously the captivity hypothesis doesn't explain why one species is more tolerant under the same captive condition.

In this study I considered several aspects of suckling behaviour. I presume that suckling behaviour and allosuckling behaviour can be influenced by the natural environment or social organization of zebra herds. While it seems that suckling behaviour was evolved under the pressure of environment, allosuckling behaviour was probably developed by the different social organization of the herd. These theories would be interesting to study among more mammalian species and subspecies differing in habitat distribution and social organization.

Studies looking for suckling bout rejection and termination and allonursing in wild equids are needed. I hope I will have an opportunity to test more parameters about suckling behaviour in future. The interesting part could be synchronization of suckling and allonursing, or the effect of activity of mare or foal on suckling behaviour. Finally, it would be compelling to study other equids species and their mother – infant interactions. Territorial species could be the first group to confirm or refuse my suggestions about social organization namely for example African wild ass (*Equus africanus*) comes from an arid environment. Studying of the suckling behaviour of these species appears to be very useful.

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8. APENDICES

8.1. Apendix 1 The Pictures of Three Zebra Species Suckling

4.6.5. Suckling of maneless zebra, photo by Michaela Olléová

4.6.6. Suckling of Grant's zebra, photo by Jan Pluháček

4.6.7. Suckling of Hartmann’s mountain zebra, photo by Jan Pluháček

4.6.8. Suckling and allosuckling of Grevy's zebra, photo by Jan Pluháček

4.6.9. Suckling of Grevy's zebra, photo by Michaela Olléová

8.2. APENDIX 2 Poster

4.6.10.Poster was presented at 38. Czech and Slovak Ethological Conference 2011

Vliv sociálního života na výskyt alokojení: příklad zeber

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Úvod

- Alokojení je kojení nevlastního mláděte cizí samicí. Bylo mnohokrát zaznamenáno u sudokopytníků[1,2,3], ale je vzácné u lichokopytníků. Dosud byly zaznamenány pouze čtyři adopce u koňovitých (zebra horská[4,5], kůň domácí[6], zebra stepní[7]).
- Rozdíly v frekvenci a délce kojení byly vysvětlovány odlišným typem prostředí[8]. V přírodě žijí zebry Grévyho (*Equus grevyi*) a zebry horské (*Equus zebra*) v aridním prostředí na rozdíl od zeber stepních (*Equus quagga*) žijících na savanách.
- Tři druhy zeber se také liší sociálním uspořádáním. Z. horské a z. stepní tvoří stabilní harémy, na rozdíl od samic z. Grévyho žijících v nestabilních asociacích.

Hypotézy

- Mládě z. horské a z. Grévyho žijící v sušších biotopech by mělo mít vyšší incidenci alokojení, a mělo by být více odmítané než mládě z. stepní žijící na savanách.
- Alokojení by mohlo záviset na sociální organizaci daného druhu. U druhů tvořících uzavřená stáda (z. stepní a z. horské) by měla být mláďata častěji odmítána cizí samicí než mláďata u druhu, kde samice tvoří pouze nestabilní asociace (z. Grévyho).

Materiál a metody

- Zoo Dvůr Králové nad Labem
- 1999 - 2002 a 2008 - 2010
- Pozorování o víkendech (08:00 – 11:00; 14:00 – 17:00)
- Zaznamenáváno vše týkající se kojení (délka, frekvence, pozice, strana, přestávky, iniciace, terminace…)
- Napozorováno 1626 hodin
- Data zpracována v SAS System, Verze 9.2.
- Použité metody: GLMM, GENMOD
- Výskyt alokojících událostí = (alopokusy + alokojení) / (pokusy + kojení)

Výsledky

$\chi^2 = 0.50$; df = 1; P = 0.47 NS

$\chi^2 = 310.75$; df = 1; P < 0.0001

$\chi^2 = 38.18$; df = 1; P < 0.0001

30 mláďat zeber stepních, 22 alopokusů, 0 alokojení

6 mláďat zeber horských, 1 alopokus, 0 alokojení

8 mláďat zeber Grévyho, 117 alopokusů, 13 alokojení

1. Našli jsme rozdíl ve výskytu alokojících událostí. Zebry Grévyho se signifikantně lišili od z. stepních a horských, ale z. horské a z. stepní se mezi sebou nelišily.

2. Samice z. Grévyho odmítaly cizí mláďata převážně odchodem, na rozdíl od samic z. stepních a horských, které je vždy agresivně odkoply (rozdíly mezi druhy–Fišerův exaktní test, P = 0,0118).

Adopce u zeber Grévyho

- V šesti měsících osiřel sameček Kevin.
- Posléze byl přijat samicí Tabií, která měla vlastní mládě (samičku) Belindu.
- Kevin byl nadále kojen společně s Belindou.

Závěry

- **Zjistili jsme vyšší toleranci samic z. Grévyho k cizím mláďatům než u z. stepních a horských.**
- **Zaznamenali jsme první alokojení u koňovitých, s výjimkou případů adopcí.**

- Nelze vysvětlit odlišnou adaptací k prostředí.

- Ale naopak se domníváme, že sociální uspořádání může silně ovlivňovat mateřské chování včetně vztahu k cizímu mláděti.

Poděkování

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Za pomoc s metodikou děkujeme Luďkovi a Jitce Bartošovým.

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