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Suckling and allosuckling in ungulates

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Habilitation Thesis

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Motto: Mnoho dat z biologie jednotlivých druhů jako je délka březosti, doba kojení či vývoj mláďat, je možno získat jedině v zoologických zahradách.

(A lot of data on biology of individual species as gravidity, time spent by lactation or the development of offspring could be received only in the zoos.)

Zdeněk Veselovský

*Suckling and allosuckling in Grévy's zebra (*Equus grevyi*) at Dvůr Králové Zoo in summer 2010*

*Suckling in common hippopotamus (*Hippopotamus amphibius*) in Ostrava Zoo in spring 2011*

Content

List of publications included into this thesis

Pluháček, J., Bartoš, L., Doležalová, M., & Bartošová-Víchová, J. (2007). Sex of the foetus determines the time of weaning of the previous offspring of captive plains zebra (*Equus burchelli*). *Applied Animal Behaviour Science, 105*, 192-204.

Pluháček, J., Bartoš, L., & Bartošová, J. (2010). Mother-offspring conflict in captive plains zebra (*Equus burchellii*): suckling bout duration. *Applied Animal Behaviour Science, 122* (2-4), 127-132.

Pluháček, J., Bartoš, L., Bartošová, J., & Kotrba, R. (2010). Feeding behaviour affects nursing behaviour in captive plains zebra (*Equus burchellii*). *Applied Animal Behaviour Science, 128*, 97-102.

Pluháček, J., Bartošová, J., & Bartoš, L. (2010). Suckling behavior in captive plains zebra (*Equus burchellii*): sex differences in foal behavior. *Journal of Animal Science, 88* (1), 131-136.

Pluháček, J., & Bartošová, J. (2011). A case of suckling and allosuckling behaviour in captive common hippopotamus. *Mammalian Biology, 76*, 380-383.

Pluháček, J., Bartošová, J., & Bartoš, L. (2011). A case of adoption and allonursing in captive plains zebra (*Equus burchellii*). *Behavioural Processes, 86*, 174-177.

Pluháček, J., Bartošová, J., & Bartoš, L. (2011). Further evidence for sex differences in suckling behaviour of captive plains zebra foals. *Acta Ethologica, 14*, 91-95.

Olléová, M., Pluháček, J., & King, S. R. B. (2012). Effect of social system on allosuckling and adoption in zebras. *Journal of Zoology, 288* (2), 127-134.

Pluháček, J., Olléová, M., Bartošová, J., & Bartoš, L. (2012). Effect of ecological adaptation on suckling behaviour in three zebra species. *Behaviour, 149*(13-14), 1395-1411.

Pluháček, J., Olléová, M., Bartošová, J., Pluháčková, J., & Bartoš, L. (2013). Laterality of suckling behaviour in three zebra species. *Laterality: Asymmetries of Body, Brain and Cognition, 18* (3), 349-364.

Pluháček, J., Olléová, M., Bartoš, L., & Bartošová, J. (2014). Time spent suckling is affected by different social organization in three zebra species. *Journal of Zoology, 292* (1), 10-17.

Gloneková, M., Brandlová, K., & Pluháček, J. (2016). Stealing milk by young and reciprocal mothers: high incidence of allonursing in giraffes, *Giraffa camelopardalis*. *Animal Behaviour, 113*(1), 113-123.

Prologue

Saturday, January, the 9th, 1999 was quite a typical day in the winter season in central Europe. The ground was covered with the remnants of snow and the air temperature was a little higher above zero. In the heated "Old Giraffe House" at Dvůr Králové nad Labem Zoo I started my observation of suckling behaviour of plains zebra. At 8:00:38 I recorded the first suckling bout. It lasted 51 seconds. It was performed by "Irbil", son of "Slávek" and "Irkasa" in the herd of maneless zebra (*Equus quagga borensis*). Since then I recorded other 4815 suckling bouts and 4297 suckling attempts in captive zebra during the following 12 years.

Analyses of that data as well as that recorded by my students resulted in 10 scientific publications which form the main content of this thesis. In addition, the thesis includes also two papers on suckling behaviour of two different ungulates: common hippopotamus (*Hippopotamus amphibius*) and giraffe (*Giraffa camelopardalis*). All these papers are based on data collected in Czech zoos. I would like to stress that ethological studies in the zoos were not favoured in Czechia/Czechoslovakia in the past. Moreover, I faced from time to time critical comments by reviewers of scientific journals that the data coming from captivity are not worthy to be published. The most common comment is that the captivity modified animal behaviour too highly. I would like to note that I did not hear such a comment over any study using data on rodents kept in laboratories or on fish in aquaria, although it could be the absence of my knowledge. I do not want to say that captivity does not modify animal behaviour. It does for sure. Nevertheless, I would like to say that it is better to study any phenomenon in captive animals than to resign to study it at all (Calisi & Bentley 2009). Moreover, the observation of zoo animals involves several advantages as we are well informed on the history of all individuals including their exact age, reproductive history or kinship.

I think that among the best examples of an animal which would be worthy to be studied in captivity is hippopotamus. To observe hippopotamuses in the wild might be quite a dangerous activity. The observed individual may easily disappear under the water full of crocodiles. It rejects all possible marking and it is able to wash the colour marking out quickly. When using telemetry, the hippopotamus destroys the collar in the water and mud environment. Last but not least, the longevity of hippopotamus is higher than that of many grant agencies.

My interest in animals was based on my frequent visits of zoos in my childhood. Later, I received nice inspiration by reading books written by prof. Zdeněk Veselovský, Dr

Luděk Dobroruka and Dr Jiří Volf (Czechoslovak researchers who worked at zoos) who supported the ethological research at zoos and considered research as one of the main role of modern zoos. I hope that the publications included in this thesis could provide at least some evidence of this role.

Acknowledgements

Introduction or why suckling behaviour and why zebras?

I would like to start this text by the explanation why I began to study suckling behaviour of zebras, and continued in the same topic in hippopotamus and giraffes. The topic of my MSc. thesis at the Charles University was the male infanticide in plains zebras (*Equus quagga*). During the study of this phenomenon I realized that the basic knowledge on suckling behaviour as the most important part of maternal investment is not very rich. Therefore, my

supervisor prof. Luděk Bartoš suggested focusing on suckling behaviour of plains zebras, I started in 1999. This allowed us to test several sociobiological hypotheses based on parent-offspring conflict theory. At the same time, many of my colleagues at the Department of Ethology, Institute of Animal Science in Prague, studied the allosuckling in even-toed ungulates. Based on more than five hundred hours of observation of plains zebras, I explained them that nobody intelligent might expect any incidence of allosuckling in this species as I observed no more than 22 attempts and all of them were rejected very roughly by the female. Within couple of months zebras themselves stopped my boasting. In the summer 2004, one of the previously observed females died and the orphaned foal was adopted by the other female including regular allosuckling. This event returned me back to the zebra stables as well as modified my comments on suckling behaviour of zebras.

I started to study plains zebra as they were (and still are) the most abundant species kept in the Czech zoos. Nevertheless, I endeavour to observe also both more beautiful "sisters" of plains zebras: Grévy's (*E. grevyi*) and mountain zebra (*E. zebra*). This happened due to the grant support for the project of interspecific comparison of suckling behaviour in equids. These observations including all three zebra species were performed also by my student Michaela Olléová. In that time, we recorded the first allosuckling incidence in Grévy's zebra as well.

In 2006, I have been appointed as European studbook keeper for common hippopotamus (*Hippopotamus amphibius*). Since the knowledge of many types of behaviour in this species (including suckling) was very poor I started to observe regularly one offspring of common hippos in Ostrava Zoo. The long evenings spent in hippopotamus house resulted in the first detailed report on hippopotamus suckling and allosuckling. Since all these publications on allosuckling (in plains and Grévy's zebra and hippopotamus) included very limited sample size (in two cases only one offspring), some of my colleagues started to say sad comments that I am an expert for studies where n = 1. In addition, they supposed that I would be incapable to verify any hypothesis explaining allosuckling on a large sample size. Therefore, I included into this thesis also our publication on allosuckling in giraffe where we found the largest incidence of this phenomenon among non-domesticated mammals and where we tested seven various hypotheses using sample size as of 37 offspring.

Besides scientific publications this thesis includes several introductory chapters. I think that this introduction should not be a simple copy of the introductions of individual publications. Therefore, I tried to include the wider context of the studied phenomena as well as some consequences of the results we found.

On importance of suckling behaviour

"Lactation is the key to sociobiology in mammals." (Wilson 1975). In most mammalian species, the lactation is energetically much more demanding than mating or gravidity. In lactation this demand is higher by 80% than in non-lactation, while pregnancy is responsible for an increase of 20% only and mating is not worthy to mention at all (Sadleir 1984; Oftedal 1985; Gittleman & Thompson 1988). The food intake increase during the lactation by 66 to 188 % according to the individual species. In addition lactating female is also highly water-dependent (Gittleman & Thompson 1988).

Moreover, lactation involves several other handicaps for the female. One of the best examples of this is the study on red deer (*Cervus elaphus*) which demonstrated that lactating hinds have lower probability to conceive in the next season, lower probability of their own survivorship to the next year, and when succeed to conceive they produce lighter offspring and later in time than non-lactating hinds (Clutton-Brock et al. 1989). Postponing of further reproduction due to lactation was documented in many other mammals (Sadleir 1984) including plains zebras we observed (Pluháček et al. 2006). Therefore, the female must take care for herself to prevent fatal exhaustion due to lactation (Rogowitz 1996). This exhaustion might happen even with sufficient amount of food and water (Bateson 1994).

Due to this demand the lactation affects the behaviour of females. They spent more time by feeding and less time by resting than non-lactating ones (Clutton-Brock et al. 1982; Green 1990). In addition, lactating females need to search richer sources of some minerals (Clutton-Brock et al. 1982). Moreover, the suckling bout itself is also risky behaviour which might attract predators, therefore it should not last too long (Drews 1991; Godfray 1991). All these limits may affect even social behaviour of the species. Thus, in some species whole groups consist only/mostly from lactating females (Sundaresan et al. 2007b; Rubenstein et al. 2015). In other species lactating individuals are responsible for the leadership of whole group (Fischhoff et al. 2007). Gittlemann and Thompson (1988) defined three main caveats with the presumption that lactation is expansive as of: (1) milk composition and quantity vary during the lactation period, (2) the higher need for energy might result from the change of other behaviours associated with maternal care and lactation, (3) lactation could vary according to the sex of offspring or litter size. It should be noted that the milk composition is not highly affected by the current food of the female even by her starvation in mammals in general (Pond 1977) as well as in equids (Pagan & Hintz 1986).

On the opposite side of lactation is a receiver of milk – the offspring. The lactation allows that the offspring receives via lactation the most of the nutritional resources which it needs at the early stages of its life (Pond 1977). By the end of lactation, the offspring might consume the same food as the parents which seems to be highly advantageous from evolutionary point of view (Pond 1977). Thus, the main evolutionary benefit of lactation is an independency of the offspring on the current availability of the food sources (Dall & Boyd 2004). This consequently allows to breed whole the year or at least to distribute parental care for the longer period (Pond 1977). In addition, due to the lactation mammals can produce relatively small offspring which grow quite quickly (Pond 1977). All these advantages of lactation do not mean that the phenomenon of lactation could be evolutionary easily explained. Since this process is very complex in terms of physiology as well as behaviourally, it remains to be advantageous only if it is carried out completely. Thus, all temporary stages are evolutionary very disadvantageous (Dall & Boyd 2004).

Considering all evidence above it cannot be doubted that the lactation represents the biggest form of maternal investment in many mammals including all ungulates (Pond 1977). Nevertheless, female should prevent to exhaust herself by lactation at least for two reasons: (1) her offspring or her relatives will need her care / help after the end of the current lactation, (2) she will reproduce in the future again, so she needs to save energy for the future reproduction. This brings conflict between her and her current offspring that requests more milk than would be advantageous to provide for the mother. The sociobiological theory which explains this as well as all variations in the tactics of mother and offspring is called as parent-offspring conflict (Trivers 1974). Briefly, this theory says 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" (Trivers 1974). The conflict is increasing with an increasing age of the offspring, because as older offspring is able to demand and receive more care / milk. This is supported by mathematical models, nevertheless the empirical studies remain scarce (Rogowitz 1996). Whereas parents have physical superiority over the offspring, the offspring needs to use mostly psychological tactics. It is quite hard to imagine better commodity in mammals that could be a subject of parent-offspring conflict than the maternal milk. The milk intake as a good example of parent-offspring conflict was mentioned in the original paper of Trivers (1974). Moreover, the female could be also involved in her internal conflict as if she would invest less (conflicting female), she would be able to produce more offspring than other (non-conflicting) female, but her offspring would face to limited survival (Fairbanks 1996). Therefore, it could be presumed that the mother would reject the

demand of her offspring less when the environmental conditions would be worse than when would be better. It should be noted that the best groups for verifying of the Triver's theory are those that produce precocial offspring and have smaller litter size (Rehling & Trillmich 2008) as ungulates.

During the 40 years after the releasing of this theory, a lot of comments including some issues were published. One issue is that neither the mother nor the offspring does know exactly the needs and possibility of their partner (Bateson 1994). Other difficulty is that the consumption of solid food is continuous process increasing with an increasing age of the offspring (Becker & Ginsberg 1990). This cause complications in measurement the conflict (Piedrahita et al. 2014). Nevertheless, despite some other comments to this theory (Mock & Forbes 1992), the Triver's theory remains the best explanation of this phenomenon.

Besides verifying the hypothesis about parent-offspring conflict, the study of suckling behaviour could be important for other reason. The suckling behaviour represents one of the basic biology characteric of each individual species. This research of basic biology of species is highly overlooked by most current scientific journals. In addition, since a lot of research is concentrated to so-called model species, our knowledge on biology of most other species remain poor. When such a study exists, it is often outdated with missing sample size and any statistics. Of course, several nice exceptions are available, e.g. suckling behaviour of feral horses is very well described by Tyler (1972). Thus, before I started this research the suckling behaviour of zebras was mentioned in only four studies (Joubert 1972; Prescott 1981; Penzhorn 1984; Becker & Ginsberg 1990), and the sample size was referred only in two of them (Prescott 1981: n = 1; Becker & Ginsberg 1990: n = 47).

Last, but not least the detailed information on suckling behaviour is necessary also for the test of those sociobiological theories and hypotheses which deal with completely different phenomena. Nevertheless, to study these phenomena the knowledge on the amount of the maternal investment is needed. These theories include e.g. male infanticide, sex ratio and allocation, selective investment, reciprocity, etc.

The mismeasure of suckling behaviour

Several characteristics of suckling behaviour could be recorded by behavioural observation. The identity of the female and the offspring are among the most important data. However, when no allosuckling occurs, these characteristics do not change in time. Within the suckling bout we can measure the following parameters: initiator of the bout, duration, frequency (or

interbout interval), position, interruptions (initiator and duration), and the animal who is responsible for the termination of the bout. Of course, it is also worthy to record whether the suckling bout was successful or it was only unsuccessful suckling attempt (rejected either by the female or by the offspring). From the most of these parameters we might presume the amount of the investment (= the amount of milk). Till now, everything looks to be quite self-evident. Longer the duration, and higher the frequency, means higher milk transferred; higher the rate of female rejection and termination mean higher the conflict over the milk. Taking into consideration these correlations published in the scientific literature that time (Duncan et al. 1984; Festa-Bianchet 1988; Becker & Ginsberg 1990; Lavigueur & Barrette 1992; Birgersson & Ekvall 1994) I had started on that grey day in January 1999 my observations of suckling behaviour of captive plains zebra recording all parameters mentioned above.

Shock therapy came quite a soon. After a couple of months of observations I read very recent (that time) publications clearly demonstrating that suckling bout duration and frequency are not good predictor of milk transfer either in mammals (Cameron 1998) or specifically in feral horses (*Equus caballus*; Cameron et al. 1999c). This was not good news for my self-confidence. It seemed that data on suckling behaviour would be scientifically almost useless. Nevertheless, lower significance of suckling bout duration and frequency for determination of the parent-offspring conflict mean at least higher importance of the rejection and termination rate of the female for the measurement of this conflict (Green 1986; Green 1990; Réale et al. 1999; Cameron et al. 2000; Cameron et al. 2003; Heitor & Vicente 2008).

In 2008, very interesting study on this topic appeared. In this experiment, the animals (white-tailed deer; *Odocoileus virginianus*) were split into two groups and one was kept on restrictive food. The calves in this group solicited for suckling more often, suckled more frequently and spent by suckling more time than those in the control group (Therrien et al. 2008). However, despite more frequent suckling these calves remained lighter in terms of their weight than those from the control group (Therrien et al. 2008). This experiment clearly showed that higher rate of suckling frequency is not related with higher milk intake but it could mean even lower milk intake as it represents hungry offspring looking for more milk as reported earlier (Mendl & Paul 1989).

It is also necessary to consider that the production of milk by the female changes during the growth of the offspring. As shown by experiments done in red deer in Spain, the amount of milk produced by the female sharply increased after the birth reaching the peak after few weeks and then slowly declined (Landete-Castillejos et al. 2000). On the other hand, milk intake of offspring increases with an increasing age of it continuously as shown in horses

(Doreau et al. 1986; Martin et al. 1992). Thus, the parent-offspring conflict (Trivers 1974) should grow especially after the milk production reach the peak.

However, the suckling behaviour is important not only for the direct investment (= for milk transfer). It has also a non-nutrition value (Trillmich 1990; Cameron 1998; Špinka et al. 2011). In several mammals even some suckling bouts might be only non-nutritive. In other species, it was documented that the offspring in stress is looking for the mother and when it reach her it takes the teat to its mouth to calm down itself (Gomendio 1990; Nicol & Badnell-Waters 2005). The best evidence for this behaviour comes from primates where frequent manipulation with mother's nipple leads to limiting of her further reproduction (Lee et al. 1991; Fairbanks 1996; Hinde 2009). Nevertheless, suckling for calming down the stressed offspring was reported for other mammals including horses as well (Nicol & Badnell-Waters 2005). In addition, the suckling behaviour might be part of other types of behaviour as play or comfort behaviour (Wolff & Hausberger 1994). Thus, even if suckling bout duration and frequency do not reflect the amount of milk transferred, they remain important parameters which might predict the psychological and social needs of the offspring (Clutton-Brock 1991; Redondo et al. 1992; Das et al. 2000).

I would like also to note that although zebra suckling behaviour was not systematically observed in the captivity before my research started, the studies which mentioned this behaviour in a qualitative way (Wackernagel 1965; Pláteník 1985; Andersen 1992; description as it looks like) concluded that it does not differ from that observed in the wild (Klingel 1969b; Penzhorn 1984; Rowen 1993).

At the Old Giraffe House in Dvůr Králové Zoo

In one of the reviews to my dissertation, very kind reviewer suggested that the text accompanying the scientific publications should include also the description of husbandry of observed animals. However, such a description cannot be used within limited space of scientific articles. Therefore, I would like to accept this suggestion and to use this space for brief description of husbandry of zebras I observed. (I omit the description of husbandry of hippopotamus and giraffes as publications based on the observation of these animals form a minor part of this thesis and the description of their husbandry would take too much space.)

All three subspecies of plains zebra (maneless zebra, Grant's zebra *E. q. boehmi*, and Chapmann's zebra *E. q. chapmanni*) we had observed at Dvůr Králové Zoo were kept under the very similar living conditions. Each subspecies was represented by one breeding herd (two

in case of maneless zebra in one season). Breeding herd included one stallion, four to nine adult mares (one herd of maneless zebra consisted of two mares only) and their offspring. Except larger number of mares in one herd of maneless zebra this social structure reflected the situation reported from the wild populations (Klingel 1967; Smuts 1976; Tong et al. 2015). Zebras inhabited outside enclosure (size: maneless zebra 1350 m^2, Grant's zebra: 650 m^2, and Chapmann's zebra 1760 m^2) and indoor stable. The entire herd was kept together in an outside enclosure as well as in the indoor space, except Chapmann's zebra where some mares were put into smaller separated space within the stable due to conflicts between them. In all plains zebra herds, the stallion was mostly together with the herd even in indoor space, but sometimes he was separated from the herd due to his aggression towards mares, especially in the night. Nevertheless, the stallion had contact with the rest of the herd via wooden bars. The animals passed from the stable either directly to the enclosure or through the small paddock in the case of maneless zebra. The zebras were confined to this paddock only very exceptionally during winter time when the enclosure was covered by ice. The timing of stay in outside enclosure was determined by the weather: from one hour till eight hours. During the summer time (from May till September), the zebras remained in outside enclosure for 24 hours. In this time Grant's zebras were confined to the small paddock for two hours at the morning due to cleaning of their enclosure.

The social organisation of mountain zebra in the wild resembles of that of plains zebra (Klingel 1969a; Joubert 1972; Penzhorn 1984). Nevertheless, their social behaviour differs in detail in some aspects and thus they have to be kept in individual separate space in indoor houses in the zoos. The only exception was the mare with her offspring (even subadult) which were kept together. During winter period the herd of mountain zebras were released into the smaller outside enclosure (1050 m^2). The herd was split and the half of the herd was in the enclosure during the morning time and the second half in the afternoon. During summer time the whole mountain zebra herd including six to seven mares, their offspring, and one to two subadults was kept in the larger outside enclosure (2800 m^2) for 24 hours. The stallion was kept within the herd only in this bigger enclosure during every second season. Due to the individual separation of mountain zebras in the stables, most of their observations were done when they were in the outside enclosures. Timing of stay in outside enclosure was the same in all three zebra species in both zoos.

All mares (from 14 to 18), subadults and offspring of Grévy's zebra were kept together in one herd within the indoor stable as well as in the outside enclosure (875 m^2). Only mares with very young foals were separated into small group and kept in separated

indoor space. This reflected their social life in the wild (Ginsberg 1989). In the stable, the stallion was separated and joined within the herd in the outside enclosure in every second season.

The same husbandry was used for Grévy's zebra at Ostrava Zoo, where the herd consisted of three mares and their two offspring kept together. The stallion was separated and joined the herd in the outside enclosure (5230 m^2) every second season. The house for Grévy's zebra at Ostrava Zoo is accessible for visitors, contrary to all zebra houses at Dvůr Králové Zoo.

All zebra enclosures in Dvůr Králové Zoo were covered by gravel and concrete without any grass. In contrast, Grévy's zebra in Ostrava Zoo inhabited fully grassed enclosure including also a small forest area. No other species except one individual of any antelope in few cases shares the outside enclosures with zebras. The hay or grass (in summer time) was provided to all zebras once a day in the morning (between 7 and 11 am) and the remnants of food were visible in the enclosures till the next morning. In addition, pellets with vitamins and carrot were provided for each zebra herd once a day. Each stable and enclosure was cleaned once a day usually at the morning and new straw was provided on the floors of stables. During summer time when zebras spent whole day and night in the outside enclosure the cleaning was performed at the afternoon as well.

Maneless and Grant's zebra were stabled in one house which they shared together with a large herd of reticulated giraffes (*G. c. reticulata*) at Dvůr Králové Zoo. Hence the internal name of this house within the zoo was "Old Giraffe House". In this house I spent the longest time by zebra observations, therefore I borrowed its name for the title of this chapter. All other zebra herds were placed in various buildings they shared with several antelope species, but not with any other equid.

On the magic sex

Among several criteria for publishing of any manuscript in scientific journals, the very important is attractiveness. I dare rather impudently to say that the most attractive effect associated with parent-offspring conflict is the sex. Of course, I think the sex of the offspring. In other words, do parents behave in different ways towards sons than daughters?

Ungulates represent a very suitable group for testing the hypotheses of selective investment into one sex because they have limited number of offspring in the litter (just one in

all odd-toed ungulates), the postnatal care is quite long, and the investment could be done via one commodity (maternal milk; Hewison & Gaillard 1999; Kojola 1999).

Among a lot of theories predicting higher selective investment to one sex over another, two are the most influential. These are Trivers-Willard model (TWM; Trivers & Willard 1973) and the Local resource competition theory (Clark 1978). Whereas the latter cannot be considered for zebra females absenting exclusive home-ranges with defended resources, the TWM seems to be very suitable for equids. TWM says that in polygynous species where reproductive success varies more among individuals of one sex than in another, parents in good condition should be selected to invest more in that sex with higher variability and parents in poor condition should invest more into the sex with lower variability (Trivers & Willard 1973). In ungulates, males represent the sex with higher reproductive variability (Clutton-Brock 1985; Rubenstein & Nuňez 2009). For TWM three assumptions must be followed: (1) The condition of the young at the end of parental investment will tend to be correlated with the condition of the mother during parental investment, (2) differences in the condition of young at the end of the period of parental investment will tend to endure into adulthood, and (3) slight advantages in condition should (because of male competition to inseminate females) have disproportionate effects on male reproductive success compared to the effects on female reproductive success. To verify these assumptions for any species is very hard work. Nevertheless, since TWM has been tested in horses many times (Cameron et al. 1999b; Cameron & Linklater 2000; Cameron & Linklater 2007; Cameron et al. 2008), it could be expected that all equids would fit these assumptions as well.

Moreover, equids including zebras has some more advantages over other ungulates to be tested in terms of TWM. These advantages include one offspring per litter, polygyny, rare occurrence of nursing non-filial offspring (allonursing, see later), and the fact that they are monomorphic. Monomorphism is advantageous because in sexually dimorphic species, the parents need to invest more in the bigger sex as offspring of this sex have to achieve bigger size in any case. Thus, it is hard to distinguish if the parents in good conditions invest more in son than to daughter because of TWM or because the son needs to be bigger per se (Lee & Moss 1986; Cameron & Linklater 2002).

Since TWM is one of the most discussed theories in sociobiology (in 1973-2017 referred 2164 times on Web of Science), I would like to avoid listing all possibilities and interpretations of this theory in hope that no critics of such an absence would be done. When using TWM over data coming from zoo animals, the problem arises as few or even no parent in poor condition could be found. I faced this problem as well. However, it was suggested that

TWM was based on long evolutionary process. Thus, most zoo animals suitable for TWM should behave as parents in good condition (White et al. 2007). Therefore, most zebra mothers in the zoo should invest more to sons than to daughters unless they drop to the poor condition. This prediction is in line with other theoretical frame (Maynard-Smith 1980) supported by some empirical studies, e.g. (Clutton-Brock et al. 1981).

In equids (specifically in horses as zebras and asses remained to be neglected by researchers studying this topic), the higher investment to sons by mothers was reported in many studies (Duncan et al. 1984; Berger 1986; Cameron & Linklater 2000; Heitor & Vicente 2008), but not all (Crowell-Davis 1985; Boyd 1988; Smith-Funk & Crowell-Davis 1992).

Based on all these presumptions, we tested whether captive plains zebra females invest more in sons than in daughters. This difference should be reflected by lower rate of suckling bout rejection and termination in sons than in daughters. Thus, we tested this and we really found the difference which was increasing with an increasing age of the foal. However, this difference was opposite to the theories mentioned above (Pluháček et al. 2010). In other words, mothers of plains zebras were more tolerant to daughters than to sons.

The easiest question is "why"? Two possible answers might clarify this situation. First, mothers try to give some advantage to daughters than to sons. Second, mothers do not distinguish over the sex of offspring but their behaviour reflects various behaviours of sons and daughters. Thus, sons could be more demanding which might result in higher mother's rate of the bout rejection and termination. I think that this second explanation is more likely in the observed case. It was later supported by two other "smaller" analyses where we found that male foals resumed interrupted bout faster than female foals and that male foals performed the same rate of attempts immediately after the successful suckling bout whereas this rate declined with the age in the female foals (Pluháček et al. 2011b). Of course, this explanation is not for science as attractive as the first one. This could be reason why it almost absents in studies dealing with suckling behaviour in ungulates (but see Lee & Moss 1986), even though the differences in behaviours of male and female offspring non-related to suckling were reported frequently (Kojola 1989; Alley et al. 1995; Cameron et al. 2008; Piedrahita et al. 2014). It should be noted that any further deeper study of this aspect could be important as an interesting case of coevolution and adaptation. It could be also hypothesised that the rejective mother might rear "bold" offspring who would apply these skills in adulthood to improve its reproductive success (Maestripieri 2004).

Thus, based on our results, I would like to emphasize that the studies on selective investment should not overlook that the final behaviour represents both sides of the conflict: the parent as well as the offspring.

One very important aspect of this selective investment should be mentioned. The milk composition the mother provides for sons and daughters may differ. This difference was reported e.g. for rhesus macaques (*Macaca mulatta*; Hinde 2009) or for red deer (Landete-Castillejos et al. 2005). In contrast, no difference was found in California sea lions (*Zalophus californianus*; Ono & Boness 1996). Therefore, our results showing no preference of sons by zebra mothers must be interpreted on behavioural level, only.

Striped horse or striped ass

"Zebra, as everybody knows, is a striped horse…" (Groves 1974). This is the start of the chapter about zebras from the excellent book of one of the best taxonomists on the world. Moreover, I choose that sentence as it reflects our attitude to zebras. Zebras stay in the shadow of their famous relative: the horse. The other smaller shadow is inhabited by their third relative: the ass. Nevertheless, in some languages like Swahili zebra is not stripped horse but stripped ass (punda milia). Thus, the question arises: is zebra striped horse or ass?

This text does not aim to evaluate all possible phylogenetic relationships among recent equids but to provide the most recent overview of them. Most recent studies are in line that equids split into two lines: caballoids including horses and stenoids including zebras and asses (George & Ryder 1986; Oakenfull & Clegg 1998; Oakenfull et al. 2000; Krüger et al. 2005; Steiner & Ryder 2011; Steiner et al. 2012). Most recent studies comparing mostly nuclear DNA (but not only) concluded that stenoids line split into two monophyletic branches; one represents zebras and the other asses (Steiner & Ryder 2011; Steiner et al. 2012; Vilstrup et al. 2013). On the other hand, almost all previous studies based on comparing of mtDNA added African wild ass (*E. africanus*) to the zebra branch and put two remaining ass species (Asiatic wild ass *E. hemionus*, and kiang *E. kiang*) as a separate line (George & Ryder 1986; Oakenfull & Clegg 1998; Oakenfull et al. 2000; Krüger et al. 2005). When comparing three zebra species, all studies came to the conclusion that mountain zebra diverged as the first and plains and Grévy's zebra split later (George & Ryder 1986; Oakenfull & Clegg 1998; Oakenfull et al. 2000; Krüger et al. 2005; Steiner & Ryder 2011; Steiner et al. 2012).

Wild equids form two different types of social organisation which are species specific (Berger 1988), and it is interesting that these types do not correspond with phylogeny of individual species. Horses, plains zebra, and mountain zebra form harems with one (more in

case of horses) adult male(s) and one to eight mares with foals (Joubert 1972; Klingel 1975; Berger 1977; Penzhorn 1984; Cameron et al. 2003; Simpson et al. 2012). In this type of social organisation mares remain together almost all life. On the other hand, males of Grévy's zebra, kiang, and African and Asiatic wild ass are solitary and protect territories (Klingel 1974; Klingel 1975; Klingel 1977; Berger 1979). Females of these species aggregate to occasional herds, where they associate for couple of days (Klingel 1974; Ginsberg 1989; Sundaresan et al. 2007a). Only a female with her last offspring associates together for longer period usually till the birth of the next offspring (Klingel 1974; Ginsberg 1989). In exceptional cases, daughter can associate with the mother longer. Thus, according to the differences in the social organisation, mountain and plains zebra cluster together whereas Grévy's zebra differs. When ecology of individual zebra species is considered, then Grévy's and mountain zebra are adapted to semi-arid environment while plains zebra live in mesic savannahs (Groves 1974; Bauer et al. 1994).

In 1990, the noteworthy study comparing suckling bout duration and frequency was published (Becker & Ginsberg 1990). Authors observed two species (Grévy's and plains zebra) and included data on other species from other studies. This might be a little problematic as various studies used various methods which makes any comparison difficult (Cameron 1998). In addition, the suckling bout duration and frequency were interpreted as the indicator of milk transfer which was common at that time (Duncan et al. 1984; Becker & Ginsberg 1990; Trillmich 1990; Green et al. 1993). Other complicated issue is the fact that the suckling bout duration and frequency might be affected by various factors like e.g. the animal terminating the suckling bout (Crowell-Davis 1985; Komárková et al. 2011; Bartošová et al. 2012) or the age of the female (Green 1990) that were neglected in this study (Becker & Ginsberg 1990).

Therefore, we wanted to compare suckling behaviour of all three species of zebra kept under the same (very similar) living conditions to verify the conclusions of previous study. When analysed the rejection and termination rate, we found that mothers of Grévy's and mountain zebra were more tolerant than mothers of plains zebra (Pluháček et al. 2012). Higher tolerance of mothers of these two species towards their foals might be explained by the fact that they evolved in semi-arid environment, where quite a strict maternal behaviour could lead to the death by starvation of their offspring. The modification of suckling behaviour as an adaptation to semiarid conditions was suggested for some ungulates in the past (Berger 1979; Becker & Ginsberg 1990).

On the other hand, time spent suckling (suckling bout duration and frequency) was longest in foals of the most "neurotic zebra species" the mountain zebra, followed by plains zebra and the shortest in the most "phlegmatic zebra species" the Grévy's zebra (Pluháček et al. 2014). In other words, these parameters reflected the tension among adult animals in the herd. In the herd of mountain zebra, the adults kept longer inter-individual distances and conflicts were rather frequent. On the other hand, we observed almost no conflicts in the large herd of Grévy's zebra. As an illustration of this "phlegmatism" of Grévy's zebra, I observed two peculiar cases of the positions for suckling. In one case, the female was lying and allowed her foal to suckle without standing herself. In the other case, it was the foal that was lying during the suckling bout. Thus, our results on interspecific comparison confirmed the hypothesis, that suckling bout duration and frequency reflects mostly social needs of offspring than the amount of milk intake (Gomendio 1990).

It is interesting that this interspecific comparison of suckling behaviour remains quite rare in mammals. Except equids, researchers compared only three species of voles (*Microtus ochrogaster*, *M. pinetorum*, *M. pennsylvanicus*; McGuire & Novak 1984; McGuire et al. 2011), and three species of macaques (*M. mulatta*, *M. tonkeana*, *M. fascicularis*; Thierry 1985), (*Macaca arctoides*, *M. mulatta*, *M. nemestrina*; Maestripieri 1994a,b). It is worthy to note that all these studies found the effect of social life on any aspect of maternal behaviour (McGuire & Novak 1984; Thierry 1985; Maestripieri 1994b; McGuire et al. 2011).

As when comparing different investment to the sex, it could be argued that interspecific differences cannot be expressed by variability in suckling behaviour only, but also in milk composition. Although some very small differences were discovered in the past, it was concluded that these closely related species produce milks which are almost identical in gross composition as well as in mineral composition (Linzell & King 1966; Schryver et al. 1986; Oftedal & Jenness 1988). Based on these small differences in milk composition Grévy's zebra clustered with asses and mountain zebra with horses (King 1965; Schryver et al. 1986; Oftedal & Jenness 1988). Thus, they correspond more with the social life of various species than reflect their phylogenetic relationships.

In the future, it would be very interesting to compare also suckling behaviour of three wild ass species. Nevertheless, to compare their suckling behaviour with our results on zebras, such an observation should be done under very similar conditions as ours. During the last observational season at Dvůr Králové Zoo we observed also 4 foals of African wild ass (*Equus africanus somaliensis*). This is of course extremely small sample size for any conclusion. In addition, asses inhabited grassed enclosure (zebras were in grassless

enclosures) which was much larger than those for zebras. Nevertheless, the pattern of their suckling behaviour was very similar to that we saw in Grévy's zebra, unrelated species living in the same biotope and forming the same social organisation…

From the left to the right or the laterality of suckling

All chapters above showed usefulness of data on suckling behaviour of zebras for the test of several theories and hypotheses. Nevertheless, these theories are more than 40 years old. Therefore, in this chapter I would like to demonstrate that data on zebra suckling behaviour might fit to test more up-to-date theories. To demonstrate this, I choose the theory of lateralisation.

The best illustration of the laterality is handedness in humans and the research on this topic is performed for a long time. The discovery of functional brain lateralisation in humans was associated with Broca's studies in the middle of 19th century (Broca 1861). The existence of structural asymmetries in the brain (particularly in the diencephalon) of lower vertebrates was common knowledge among neuroanatomists at the beginning of the 20th century (Rogers & Andrew 2002). However, subsequently any mention of these asymmetries disappeared from the textbooks and remained forgotten for long time. Thus, the research on lateralised behaviour in non-human beings is quite young and started at the beginning of eighties (Denenberg et al. 1980; Denenberg 1981; Andrew & Brennan 1983; Denenberg 1983), reaching the peak in the first decade of this century (Rogers & Andrew 2002; Rogers 2010). In addition, studying of lateralised behaviour results in several practical outputs like indication of welfare for captive animals (Rogers 2010; Zucca et al. 2011) as well as during the training of animals (Rogers 2010).

Lateralisation might be expressed on two different levels: on the population level and on the individual one. The lateralised behaviour on the population level is based on brain asymmetries and subsequently on the asymmetries of sensory organs (MacNeilage et al. 2009). The most intensive studied sense in this aspect is the vision. Asymmetries performed by vision are affected by optic decussation, thus the stimuli taken by left eye are processed mostly in right hemisphere and vice versa (Rogers 2010). In most animals, the left hemisphere (~ right eye) is responsible for proactive behaviour, learning abilities, searching for food, for partner, etc. (Rogers & Andrew 2002). On the other hand, the right hemisphere (~ left eye) is responsible for reactive behaviour, thus affected mostly by outside stimuli, for immediate response or species-specific behaviour (Rogers 2010). The stimuli coming from left eye (right

hemisphere) are important for individual recognition in ungulates, primates or birds (Rogers & Andrew 2002; Rogers 2010). In addition, imprinting, ambiguous behaviour, mating behaviour, and aggressive behaviour are proceed mostly by the right hemisphere as well (Austin & Rogers 2012). Since the suckling behaviour is a part of the parent-offspring conflict, it could be presumed that it would be advantageous for the young to be detected by the mother's right eye first when approaching toward her than by her left eye (Rogers & Andrew 2002).

The other level of the lateralisation is the individual one. The best expression of this is the handedness in humans. Also in non-human animals most studies measured this lateralisation by preferential using of right or left limb (Williams & Norris 2007). Individual lateralisation is quite an advantageous strategy as demonstrated either by empirical studies or by theoretical models where it is considered as an evolutionary stable strategy (Rogers & Andrew 2002). Since individual lateralisation is species-specific, every study on this topic in any unrepresented species might be of common interest (McGreevy et al. 2007; Rogers 2010).

Although most mammalian species posses even number of nipples sorted in two rows, it is surprising that only few studies focused on lateralisation of suckling behaviour. Till now, almost all studies on this topic were performed on primates. Nevertheless, primates are not a good model for studying this topic because they have not monocular vision and the active assistance by the mother form an important part of their suckling behaviour (Nishida 1993). However, research on primates offer the higher number of scientific journals where the results might be published. Moreover, various empirical studies on lateralisation of suckling behaviour in primates came to different conclusions (Nishida 1993; Damerose & Hopkins 2002; Hopkins & De Lathouwers 2006; Jaffe et al. 2006). On the other hand, the suckling behaviour of equids represents very good opportunity for testing the lateralisation of suckling behaviour, because of lateralised position of eyes and due to antiparallel position which is the most common for suckling (94.1%, n = 5301; Pluháček et al. 2013). In this position, the foal stands by the mare but his head is directed towards the rump of the mare. Thus, it is very easy to define left and right side.

Before our research, only one study briefly reported on the lateralised suckling behaviour in domestic horses. This study revealed small preference for successful suckling from the right side on the population level (Carson & Wood-Gush 1983).

When we tested lateralisation in all three zebra species, no side preference was detected either for successful suckling bouts or for unsuccessful suckling attempts on the population level (Pluháček et al. 2013). However, we found individual lateralisation in 10 out

of 35 observed foals. This laterality increased sharply with the increasing age of the foals. I have to write that I have been personally surprised by these results as I did not mention them during the observations (they appeared after the data analyses). This could be done by the fact that when observing zebras I did not know any theory about laterality, so I recorded data about laterality only as one of several descriptive traits.

Two interesting consequences might results from our findings. First, since the lateralisation of suckling was strengthened with increasing age of the foal, this behaviour is learnt and not innate. This is in line with other studies on lateralised behaviours (but not suckling) of equids (McGreevy & Rogers 2005). Second, we found that the rejection rate by the mother was higher in foals which showed any lateral preference than in foals without preference. Although during the suckling bout the foal can reach both teats it is very likely that it uses mostly the teat which is closer. If so, then it seems that lateralised preference of suckling is a little painful for the mother and hence she refuses more suckling solicitations.

At the same time when we performed this research my colleagues observed suckling behaviour including lateralisation in domestic horses (Komárková & Bartošová 2013). They came to the very similar findings as we did on zebras. Thus, I can conclude this chapter by simple statement that from the point of view of lateralisation of suckling behaviour, the horse remains only stripeless zebra.

Allosuckling as the extreme investment

Allosuckling is defined as suckling of non-maternal offspring and similarly allonursing is nursing of non-filial offspring. As lactation is energetically the most demanding part of the female reproduction in many mammals, the allosuckling represents the extreme of such an investment (Packer et al. 1992). Since the production of milk is costly, it could be expected that the allosuckling would occur rarely. Despite of this expectation, the allosuckling was recorded quite often mostly in carnivores, especially in pinnipeds, in rodents, and in even-toad ungulates (Packer et al. 1992).

The highest incidence of allosuckling was recorded in domestic animals, perhaps because they produce more milk when compared with their wild counterparts of the same size (Oftedal 1984). In wild animals, higher incidence of allosuckling was reported in captivity than among wild populations (Packer et al. 1992). It is more common in polytocous species than in monotocous ones, in those that form breeding groups or colonies (Packer et al. 1992),

and in those which wean the offspring sooner than in species with long lactation period (Pusey & Packer 1994).

Several hypotheses explaining why females would invest into non-filial offspring were formulated. These hypotheses are not mutually exclusive and their support by empirical data varies highly (Roulin 2002; Maniscalco et al. 2007). These hypotheses might be divided according to the adaptiveness or whom motivation they explain (either female or offspring). Two non-adaptive (misdirected parental care and by-product of living in the group) and five adaptive (reciprocity, kin-selection, milk evacuation, parenting, and social benefit) hypotheses were postulated to explain allonursing by the female (Hayes 2000; Roulin 2002; Baldovino & Di Bitetti 2008). It should be noted that three other adaptive hypotheses were suggested in the past. Nevertheless, they have not been emphasized enough in the very important review on allosuckling published in 2002. Therefore, further studies did not consider them as the potential explanation. These hypotheses are: (1) development of future ally (Mann & Smuts 1998), (2) avoid disturbing of their mating cycle by adoption and allonursing (Riedman & Le Boeuf 1982), and (3) to calm a stressed juvenile (Lee 1987). The allosuckling by an offspring could be explained by four hypotheses: to improve immune system (Roulin & Heeb 1999), to steal the milk (theft hypothesis; this is tactic and not the reason; Packer et al. 1992), to compensate of low birth mass or inadequate growth (Víchová & Bartoš 2005), and to improve nutrition (Engelhardt et al. 2016a).

The aim of this text is not to describe all individual hypotheses, their advantages and disadvantages as this was done in several recent papers (Engelhardt et al. 2015, 2016a,b; Gloneková et al. 2016). Instead, I would like to stress the variation of support of individual hypotheses by studies using empirical data. In general among mammals, the highest support received the theft hypothesis (Packer et al. 1992; Maniscalco et al. 2007; de Bruyn et al. 2010; Brandlová et al. 2013). Both reasons for theft either the improved nutrition (Engelhardt et al. 2016a) or compensation low birth mass, low milk income or inadequate growth (Víchová & Bartoš 2005; Zapata et al. 2010) were supported almost equally. By the way, one part of the compensation hypothesis can be used as a nice example why allosuckling might be useful for explaining some basic suckling parameters. In cattle (*Bos taurus*) it was reported that high suckling bout frequency in lighter offspring could be caused by higher and vain effort of these offspring to receive more milk (Víchová & Bartoš 2005). In other words, the higher frequency of suckling or allosuckling did not mean higher milk intake.

Mammalian females allonurse mostly because of misdirecting their care (Franco-Trecu et al. 2010) or to support their kin (kin selection hypotheses; Engelhardt et al. 2016b).

On the other hand, reciprocity as a main reason for allonursing was documented only few times. It is worthy to note that many times it is difficult to distinguish between reciprocity and kin selection hypotheses as the most allonursing species form the groups consisted from relatives. Also the hypothesis of social benefit was verified rarely, but it should be noted that it was not tested very often. Almost no support was found for parenting hypothesis.

Two remaining hypotheses - milk evacuation and improve immune hypotheses - are very difficult to be tested. Therefore, they appear time to time as possible explanation for allosuckling, although direct evidence is poor (milk evacuation hypothesis) or even missing (immune hypothesis).

Among even-toed ungulates, the highest support received the kin-selection hypothesis (Ekvall 1998; Bartoš et al. 2001; Engelhardt et al. 2016b), milk-theft hypothesis (Zapata et al. 2009b; Brandlová et al. 2013), either for nutrition improvement (Engelhardt et al. 2016a) or due to compensation (this hypothesis was suggested for them: Bartoš et al. 2001). Milk theft is often accompanied (but not in all cases, see: Zapata et al. 2009b) with misdirected care by the female.

Allosuckling remains to be extremely rare among equids despite very intensive observation of their suckling behaviour mostly in feral or domestic horse (Tyler 1972; Feist & McCullough 1976; Schoen et al. 1976; Crowell-Davis 1985; Barber & Crowell-Davis 1994), In total, only 4 cases were known (except our studies) and all of them included adoption (King et al. 2016). Two cases occurred in mountain zebra (Lloyd & Harper 1980; Penzhorn 1984) and two others in feral horses (Cameron et al. 1999a; Nuñez et al. 2013). The later ones are interesting as they compared several parameters of allosuckling with those of the suckling of own offspring. Whereas one study dealing with typical case of adoption did not reveal any differences between allosuckling and suckling (Nuñez et al. 2013), the other one reporting simultaneous suckling of one foal by two mares (mother and grand-mother) found interesting results. The rejection and termination rate of both mares was much lower than in all other mares (Cameron et al. 1999a). Two conclusions may result from this finding. First, this illustrates the importance of rejection and termination rate for studying suckling behaviour as maternal investment. Second, this stresses the importance of such an extreme case (allosuckling) for better understanding of suckling behaviour including parent-offspring conflict.

When the case of adoption of the orphaned foal involving regular allosuckling occurred in the herd of Grant's zebra in Dvůr Králové Zoo, it was impossible to me to ignore it. Our study represents the first report of adoption and allosuckling in plains zebra (Pluháček

et al. 2011a). Nevertheless, we found one more interesting result. The duration of suckling bouts was almost by one third shorter in the mare which nursed two foals than in those that nursed only one foal. In addition, the suckling bout duration when both foals suckled at the same time was shorter than when only one suckled, when considering either the foals nursed by the allonursing female only or other mare-foal pairs. Moreover, as expected the mare nursing two foals within one season rejected suckling attempts and terminated suckling bouts more often than when she was nursing a single foal. Recently, the study on allosuckling in reindeer (*Rangifer tarandus*; Engelhardt et al. 2014) reported that suckling bout duration decreased with an increasing number of (allo)suckling calves. Similarly, in warthogs (*Phacochoerus africanus*) the time spent by suckling decreased with increasing number of juveniles and the allosuckling bout duration increased with increasing inter-bout intervals (Plesner Jensen et al. 1999). When considering all these results together it seems that under extreme conditions (allosuckling) the big differences in suckling bout duration are likely to reflect milk intake.

Several years after this case we observed unusual case of adoption in Grévy's zebra (Olléová et al. 2012). This adoption occurred in foal of the age of several months. In addition, the adoptive mother had her own foal, therefore in this case we cannot explain the adoption by misdirected care of the mother. Moreover, Grévy's zebra foals allosuckled unless to be adopted. These cases were the first of their kind among intesivelly studies equid species. The possible explanation of quite frequent occurrence of allosuckling in Grévy's zebra compared with other equids might be in different social life of Grévy's zebra. Mares of Grévy's zebra associate together only for couple of weeks (maximum are two months in early lactation; Ginsberg 1989), therefore misdirected care should not be energetically as demanding as in species forming stable harems. This explanation is in line with the previously mentioned general suggestion that social organisation is very important for understanding interspecific differences in parental behaviour.

In conclusion, the allosuckling in equids remains very rare phenomenon. Nevertheless, each of these cases represents very important event and the results taken from these extreme situations might be very helpful in our understanding of suckling behaviour in general.

On allosuckling of mysterious river horse and elegant beauty that forgot to count

African lakes and rivers are inhabited by a large megaherbivore using from the time of Linné the scientific name *Hippopotamus amphibius*, which is derived from old Greek and

means "river horse" who is able to live "both lives" i.e. in the water as well as on the land. Since common hippopotamus lived in Nile in Ancient Egypt (Manlius 2000), it was well known to all old civilisations. It is also very widespread in the captivity (Pluháček 2017). Despite these facts, our knowledge on many aspects of biology of this species remains quite poor and common hippopotamus represents a little mysterious animal. The following facts were known on its suckling behaviour: it occurs in the water (Vosseler 1923; Vevers 1926; Verheyen 1954) as well as on the land (Bartlett 1872; Sokolowsky 1915; Verheyen 1954), the female takes her position as lying on her flank (Bartlett 1872; Verheyen 1954), and the suckling bouts last around 3 - 4.5 minutes (without referring the number of observed animals or bouts). All the research on this topic was done before 1954.

Therefore, I hope that our detailed observation of suckling behaviour of captive hippopotamus was important, although it involved only one offspring. In addition, this offspring was also allonursed by its grand-mother, so we recorded the first case of allosuckling in common hippopotamus as well (Pluháček & Bartošová 2011).

Since this study was based on extremely limited sample size, it is impossible to try to explain this case by any hypotheses except rejection of parenting hypothesis in the case of hippopotamus grand-mother. Nevertheless, I would like to mention three aspects derived from this study which might be of interest.

First, the lactating female is highly dependent on water intake. Since common hippopotamus spent more time in the water than on the land, this resource is not so limiting for such a species. Therefore, allosuckling does not need to be as costly issue for common hippopotamus as for terrestrial ungulates.

Second, when suckling bout is occurring in the water, both participants (female and offspring) must be submerged and they emerge regularly. I recorded also intervals between two consequent emergences of both participants within the suckling bout. We found that the calf emerged more often than the female. Nevertheless, more interesting fact was that the interval between last two emergences of the calf was two times longer than all other intervals between two emergences. Based on my observations I am not able to say why the calf did this. Nevertheless, the closest relatives of hippopotamuses - cetaceans (Geisler & Uhen 2003; Geisler & Theodor 2009; Orliac et al. 2010; Boisserie et al. 2011) as well as animals which were considered as their closest relatives till the 90th - pigs (Boisserie et al. 2011) have interesting pattern of suckling bout. In both of these groups the offspring needs perform the massage of the teat / udder, and after this the female ejects the milk (Jensen 1988; Peddemors et al. 1992; Miles & Herzing 2003; Špinka et al. 2011). It is likely, that the hippopotamuses

share the same pattern of suckling bout. This is supported by our results showing short intervals between emergences and the very long last interval.

Third, the lactation status of the female was used as a methodological tool for description of reproductive biology of the species. Most studies on this topic were published from 1960 till 1980 and they were based on harvest of hundreds of shot hippopotamuses. The dead bodies were investigated and the rate of pregnant and lactating females was used for computing the age of fertility and fertility rate of the species. These results remain still valid. However, if the allosuckling would be more widespread in common hippopotamus then these data would be doubtful. It is worthy to mention the discrepancy among data on reaching the fertility in hippopotamus from the wild and from the captivity. Whereas in captivity we collected very exact data and we know that females could conceive successfully when at her age of 2 years and 3 months, and males are fertile when at the age of 2 years and 9 months (Dittrich 1976; Pluháček 2017), the data from the wild are estimates based on tooth wearing. According to these studies, the age of the first conception is from 6 to 15 years (mean 9 years) for females and from 6 to 13 years (mean 7.5 years) for males (Laws & Clough 1965; Laws & Clough 1966; Sayer & Rahka 1974; Marshall & Sayer 1976; Smuts & Whyte 1981). Although, I admit that animals in captivity might mature more quickly than in the wild I do not believe that the difference could be so huge. I used this example to illustrate why it might be important to study animals, especially mysterious large mammals, in zoos.

I intended to avoid explaining allosuckling by any hypotheses in zebras and in hippopotamus because of very limited sample size in all these studies. On the other hand, in the case of giraffe we found the highest incidence of allosuckling among non-domesticated animals which allowed us to test seven hypotheses. We confirmed milk theft hypothesis and found partial support for reciprocity (Gloneková et al. 2016). We found that the giraffe "A" allowed to allosuckle to the offspring of her partner "B" at least once was when the calf of "A" successfully allosuckled at least once in female "B" as well. However, we did not support the biological market theory (Noë & Hammerstein, 1994) as no evidence was found that if the female allonursed more, her calf was accepted more time by a partner female. We ascribed this result to the fact that a giraffe female cannot determine how much milk her calf has received from another female, but she is able to identify from which female her calf received the milk. In addition, it is likely that in the wild the allosuckling is not as widespread as in captivity. To follow biological market theory these elegant beauties (giraffes) had to be selected to the skill of counting (at least allosuckling bouts). I personally doubt that such a selection occurred.

Shortly before the publication of our study the reciprocity was supported as an explanation of allosuckling in reindeer (Engelhardt et al. 2015). This shows slightly increasing support for this hypothesis in the recent years. In general, giraffes which form the herd consisted of both related as well as unrelated individuals within "fission-fusion" social life (Bercovitch & Berry 2013; Carter et al. 2013), seem to be very interesting species for further testing the hypotheses explaining allosuckling.

For the test of allosuckling hypotheses in giraffes we used suckling bout rejection as other researchers did (Zapata et al. 2009b). Suckling bout termination could not be used as females terminated most number of bouts (93.5 %, n = 1102). Nevertheless, in the future we would like to analyse the suckling bout duration and frequency to find out whether the same hypotheses would be supported by analyses of other suckling parameters or not.

Intentionally, I finished this text by description of allosuckling of three phylogenetically distinct ungulate species: Grévy's zebra, common hippopotamus, and giraffe. In Grévy's zebra we revealed the highest incidence of allosuckling among equids, in giraffe the highest incidence of allosuckling among non-domesticated mammals, and the incidence of the allosuckling in common hippopotamus would be a very speculative topic. Nevertheless, this species was almost not studied in the past. Although evolutionary distinct all these three species share one ethological trait: they form "crèche" (Verheyen 1954; Klingel 1974; Pratt & Anderson 1979; Becker & Ginsberg 1990). In crèche one or more adults guard several offspring. In the case of Grévy's zebra all lactating mothers travel for hours to the water source leaving their offspring in the crèche (Ginsberg 1989). This is the excellent predisposition for development of allosuckling based on reciprocity. As a conclusion, I would like to stress that the occurrence of allosuckling might be affected more by social organisation of the species than its position in phylogenetical tree.

It could be objected that all these results came from captivity and therefore it may represent more artificial behaviour completely different from the behaviour seen in the wild. Although the effect of captivity cannot be neglected, it should be mentioned that allosuckling was observed in the wild in giraffes (Pratt & Anderson 1979), in Grévy's zebra (Becker as pers. comm. in Packer et al. 1992), as well as in other species that were reported frequently to allosuckle in captivity like guanacos (*Lama guanicoe*; Zapata et al. 2009a). The suspicion of the incidence of allosuckling was suggested for wild common hippos as well (Smuts & Whyte 1981). Thus, the effect of captivity can strengthen the behavioural trait, but it cannot be responsible for its appearance (Birgersson et al. 1991). In conclusion, I would like to

emphasize that our knowledge on allosuckling of most ungulates would be extremely weak without observation of captive animals.

Epilogue

The cloudy sky evoked huge forthcoming storm on Sunday afternoon, the July, 18th, 2010, although the air temperature was quite nice: 20°C. At 16:42:09 the maneless zebra female "Karmel" terminated by leg movement the suckling bout of her daughter "Misty", the daughter of the stallion "Israel". This was my last record of suckling bout of any zebra foal in Dvůr Králové Zoo. It took another 13 months when I recorded the last suckling bout of Grévy's zebra at Ostrava Zoo where I am based now. This was the end of the interesting period, which allowed me to see some hidden aspects of the zebra's life.

It seems to be an irony that most of the data I collected cannot be recorded anymore under the same environment. Several exhibits were rebuilt in Dvůr Králové Zoo. These renovations led to the improvement of the animal welfare as well as of visitors watching places. However, the new design of enclosures prevents from the future observation of zebras. In Ostrava Zoo, the hippopotamus house was renovated as well with the same results – better living conditions for animals and experience for visitors, but it is impossible to observe the hippopotamuses underwater anymore. Last, the pressure of public opinion in hypersensitive Europe almost stopped the reproduction of giraffes in European zoos. Therefore, only few zoos allow seeing more than one giraffe offspring in one herd.

This does not mean that the follow-up research would be impossible. It is possible and some of my students are involved in this. I hope that it is clear from this text that the observation of suckling behaviour of three wild ass species would be the most interesting topic of future studies of suckling behaviour in equids. Further studies that would record allosuckling events of other even-toed ungulates that remain "similarly forgotten" as hippopotamus or giraffe could help to clarify our knowledge on this phenomenon.

Nevertheless, I hope that I took and used the opportunity to study suckling and allosuckling behaviour in captive zebras, hippopotamus and giraffes at right time to improve our knowledge on parent-offspring conflict in general.

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