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Reproduction of domestic horses (*Equus caballus*): The effects of inbreeding, social environment and breeding management

Ph.D. Thesis

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ANNOTATION

This thesis is focused on horse social behaviour and reproduction under human management. First part of the thesis covers issues about reproduction influenced by humans, breeding in restricted areas and artificial processes which can interfere or threaten the domestic horse population survival. These issues are described in lifetime order from conception, through lactation and maternal investment up to weaning, and on the background of detailed information about particular individuals. The second part is focused on social interactions and forming dominance hierarchy within the groups of domestic horses.

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Jana Dubcová

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The authors of pictures used in the text are Martina Komárková and Jana Dubcová. The pictures were made during the observations, so Kladruby horses, which are the main 'actors', are depicted there.

LIST OF PAPERS AND AUTHOR'S CONTRIBUTION

The thesis is based on the following papers (listed thematically):

① Komárková, M., Bartošová, J., **Dubcová, J.**, (2014). Age and group residence but not maternal dominance affect dominance rank in young domestic horses. Journal of Animal Science. 92:5285-5292. *(IF 1.92)*

② **Dubcová, J.**, Bartošová, J., (*in prep*). Lower reproductive success in highly inbred domestic horse mares: A message from 70 years of breeding history of an endangered population.

(3.1) Bartošová, J., Komárková, M., **Dubcová, J.**, Bartoš, L., Pluháček, J., (2011). Concurrent lactation and pregnancy: pregnant domestic horse mares do not increase mother-offspring conflict during intensive lactation. PloS one, 6(8), e22068. *(IF 3.534)*

(3.2) Komárková, M., Bartošová, J., **Dubcová, J.**, (2011). Effect of mares' dominance rank on suckling behaviour in the loose housed domestic horses. Applied Animal Behaviour Science. 133, 54– 59. *(IF 1.626)*

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⑤ **Dubcová, J.**, Bartošová, J., Komárková, M., (*in prep*). Impact of Inbreeding on Social Behavior and Dominance Rank in an Inbred Population of Domestic Horses (*Equus caballus*).

CO-AUTHORS AGREEMENT

Ing. Jitka Bartošová, Ph.D. and Mgr. Martina Komárková, Ph.D., as the first authors of the papers 1, 3.1 and 3.2, as well as the main co-authors of the papers 2, 4 and 5 fully acknowledge the contribution of Jana Dubcová on these manuscripts. They confirm, that the participation of Jana Dubcová corresponds with the number of co-authors and their order. They also confirm, that Jana Dubcová participated in all stages of the preparation of all publications listed above, *i.e.* data collection and management, statistical analyses and results formulation, writing the publications and final adjustments during the review and publication processes. They hereby agree with publication of the papers in this thesis and support this statement with their signatures.

Mgr. Martina Komárková, Ph.D

Ing. Jitka Bartošová, Ph.D.

CONTENTS

1. INTRODUCTION

Present thesis is focused on horse social behaviour and reproduction under human management. It covers issues about reproduction influenced by humans, breeding in restricted areas and artificial processes which can interfere or threaten the domestic horse population survival. It also deals with social interactions and forming dominance hierarchy within the groups of domestic horses.

Captive populations suffer from similar problems as small populations living under natural conditions. Both of them are endangered with extinction because of low genetic variability and wild ones may suffer also from habitat losses (Brook et al., 2002). Also the domestication instigated changes into horses' lives as many of its aspects are in conflict with the adaptive behaviour of the horse (Goodwin, 2002). This was occurred because of taking horses from original natural environments, to conditions which are suitable for humans, led to restrictions of many aspects of horse behaviour (Goodwin, 2002). Nowadays humans may control horses' freedom in general, *i.e*. choice to choose food, shelter, mates and social companions (Goodwin, 2002). These restrictions and human disruptions may cause problems or undesirable changes not only with horses' reproduction but also with horses' social and spatial organization, and they can further threatened the population survival. The other consequence of domestication is lowered patrilinear genetic variability as a result of specific way of horse domestication with few stallions genetically contributing to the domestic horse (Lindgren et al., 2004; Lippold et al., 2011a).

The hundreds of breeds of domesticated horses are generally bred in separated groups, but on the other hand, they do not necessarily have a clear and direct history and only rarely they are genetically isolated from the rest of the remaining population (Cieslak et al., 2010). The preferential mating of relatives has been used in horse husbandry for breed improvement and for maintaining specific heritable traits, which define particular breeds (Kristensen and Sorensen, 2005; Cieslak et al., 2010). All these processes have left their vestiges inside the genetic pedigree of the domestic horses (Cieslak et al., 2010) and many breeds of horses are more or less inbred (e.g. Cervantes et al., 2008; Bhatnagar et al., 2011; Vostry et al., 2011; Binns et al., 2012). Moreover it has been reported, that lowered genetic variability (*i.e*. high inbreeding levels) can negatively influence many fitness characteristics in various species as well as horses (Lacy, 1997; Keller and Waller, 2002).

For the present study we used the Kladruby horse, a native Czech breed, that comprises only of about 1500 individuals registered in studbook (Dyková et al., 2010). The breed was founded in 1579 by Kaiser Rudolf II. and has been bred in National Stud in Kladruby nad Labem, which was declared together with Kladruby horse as a national cultural monument in 2002 (Dyková et al., 2010). Although this breed passed through several bottlenecks (Dyková et al., 2010), its average inbreeding coefficient (0.076) is similar to other breeds (Vostry et al., 2011), e.g. Spanish Arab Horse (Cervantes et al., 2008). However, inbreeding levels causing reproductive failures in horse is even lower (around 0.04) (Klemetsdal and Johnson, 1989), so Kladruby horses may suffer from inbreeding depression

These facts provoke the need of detailed analyses of behaviour and reproduction including rearing the young. This experimental study is unique, because it describes an influence of human management on horse reproduction from conception through lactation and maternal investment up to weaning and also uncover both positive and negative influences on horse social behaviour and success. The unique environment in the National Stud served well for studying sufficient numbers of socially interacting horses in relatively invariable environment with the background of detailed information about particular individuals. So it was possible to investigate following topics: (1) If the maternal dominance position, plus differences in suckling parameters or maternal style, may stay behind later outcome of the offspring's dominance position; (2) If the inbred mares are less successful in offspring production; (3a) How the pregnant mares that suckle the foal, cope with double maternal investment; (3b) If there are any differences in maternal investment among mares, and if so, if they are dependent on their dominance rank; (4) If there are any differences in post-weaning growth in the foals based on weaning management.; (5) If the more inbred horses are less successful in obtaining higher dominance position and if they invoke and participate in less social interactions than less inbred ones.

Finally, it is known that the environmental and demographic characteristics of horse populations varies greatly (Linklater et al., 2000), but the social and spatial organization and behaviour of horses probably resemble their ancestral, pre-domestic condition and they have been believed to be largely unaltered by domestication and artificial selection (Feist and McCullough, 1976; Linklater et al., 2000). Therefore the results and conclusions obtained in this study about small population of captive horses can be applied also on feral horse populations or to other equid or mammalian populations with similar social structure in general.

1.1. HORSE FROM THE PAST TILL NOW

'They were in their heyday in Miocene but today only the negligible shine remains.'

The *Equidae*, a family within the odd-toed ungulate Order *Perissodactyla* (which includes rhinoceroses, tapirs, and other closely related extinct groups), was widespread from Eocene till Pleistocene, but today consists of the single extant genus *Equus* (MacFadden, 2005). This genus is separated, on the basis of morphological differences, in three deep clades, *i.e*. caballines (*Equus*), zebras (*Hippotigris*) and asses (*Asinus*) (MacFadden, 2005).

Evolution of the *Equidae* has begun around 55 ma BP. From ca. 57 to 25 ma BP. *Equidae* were herbivorous browsers of relatively small body size but during the early Miocene (ca. 25-15 ma BP.) came the major pulse of body mass evolution simultaneously with the principal taxonomic diversification of both browsing and grazing horse-like forms (MacFadden, 1986). This trend of body mass increase continued during the later Miocene to the Pleistocene with growing numbers of browsers/grazers and mixed feeders (MacFadden, 2005).

Equidae (*Equus ferus*) originated in North America (NA), then migrated to the eastern Eurasia and it expanded to western central Eurasia (MacFadden, 2005; Warmuth et al., 2012). Around 10,000 years ago they died out in The New world; the reasons of extinction are still discussed. Recently it has been accepted, that the humans probably did not cause the extinction of prehistoric horse in NA only because there is a hiatus (gap) between the last dated horse and the earliest undisputed human artefacts (Guthrie, 2003). Also another example used - rapid decline in body size before extinction - is not clear, because this decline is best attributed to a coincident climatic/vegetational shift in late Pleistocene (around 15,000 years BP.) (Guthrie, 2003). The climate in NA in this time shifted away from intensely arid steppe conditions (cold Mammoth Steppe), which the equids were well-adapted, to more moisture and warmer conditions (Guthrie, 2006) with lakes, bogs, shrub tundra, forest and low-nutrient acidic soils (Bigelow and Powers, 2001). So the reason of extinction of equids in NA was probably the combination of multiple climate/vegetational changes causing increased competition with other large mammals possessing the physiological capacities to thrive on the vegetation characteristics of this end-Pleistocene transition (Guthrie, 2003; 2006).

Somehow reverse process occurred with equids on the other side of the world, in Eurasia. As reviewed in Bendrey (2012), after arrival to the eastern Eurasia equids expanded to almost whole continent and became abundant in Late Pleistocene. However at the start of Holocene when the climate get warmer as a result of ending Ice Age and the cold open steppes changed to tree-dominated landscapes, horses disappeared in many places in competition with fauna more suited. In this time they met humans, who hunted them for meat, but on the other hand they tried to tame them (Levine, 1999), so the process of domestication could start and the numbers of horses started to increase (Bendrey, 2012). What happened to wild population of horses in Europe following the appearance and spread of domestic animals is unclear (Bendrey, 2012).

Price (1984) defines domestication as a process by which a population of animals becomes adapted to man and to the captive environment by some combination of genetic changes occurring over generations and environmentally induced developmental events reoccurring during each generation. Thus the domestication is slow and long-lasting process of 'adaptation'. Human used and are still using horses for many purposes, *i.e*. as a source of meat, milk, coat; means of transport, labour; for fighting in some cultures; and as a 'pet' (Levine, 1999). However the process of domestication still have some questions with four main ones - where, when, how and from which 'species' of *Equus* horses were domesticated - discussing in many papers with using different evidence from bones and artefacts through damaged skeletal tissues in the mouth indicating using a bit, up to traces of fatty acids from horse milk etc. (e.g. Levine, 1999; Outram et al., 2009; Bendrey, 2012; Warmuth et al., 2012). Finally it has been suggested that the origin of domestication of wild horse (*Equus ferus*) was in western central Eurasia about 5,500 years ago (Outram et al., 2009; Warmuth et al., 2012) and that spread of horse domestication out of this region involved both actual population movement and introgression from the wild which was necessary for maintain or grow herd sizes (Warmuth et al., 2012). However the demography of horses changed markedly following domestication. Compared with the expansion of *E.ferus*, the spread of domestic horses was characterized by weaker founder effects and smaller effective sizes of established populations (Lippold et al., 2011a).

Two big population bottlenecks in horse history are known - mass extinction of large-bodied mammals (10,000 years ago) and domestication (Kavar and Dovc, 2008). Both bottlenecks decrease the number of survived haplotypes (and their derivatives) which can be found in recent domestic horses (Kavar et al., 2002) but they had different consequences for paternal and maternal lines (Kavar and Dovc, 2008). Since the stallions are inherently more difficult to handle than mares (Lippold et al., 2011a) and due to the social organisation of horses where one sire is enough for mating a multiple mares (Lindgren et al., 2004), they were the mares who were mostly domesticated. Thus the matrilinear base of domestic horses came through domestication with high diversity (Vila et al., 2001; Cieslak et al., 2010; Lippold et al., 2011b), but the patrilinear one lost a lot of its diversity from pre-domestication (Lindgren et al., 2004; Kavar and Dovc, 2008; Cieslak et al., 2010; Lippold et al., 2011a).

Although much inconsistence in the taxonomy of both extinct and living horses exists (e.g. McCue et al. (2012); Orlando et al. (2013); Vilstrup et al. (2013)) it seems that present domestic horses originated from steppe form of tarpan (*Equus ferus ferus*) and that the present only 'wild' horse - Przewalskii horse (*E. ferus przewalskii*) can be involved in (summarized in Robovský, 2009).

After 5,500 years of horse husbandry, the world is populated by more than 58 million of domestic horses [FAO Statistic Division 2014 for 2013; http://faostat.fao.org]. The exact number of breeds is impossible to determine, but ranges from 600 up to 1000 breeds (some of them are primitive breeds known since ancient times, others were founded a few decades ago) (Cieslak et al., 2010). Nevertheless the situation of true wild horses is shattering. Tarpan (*E. ferus ferus*) became extinct in Europe at the beginning of the 20th century (Kavar and Dovc, 2008). However some attempts were undertaken for its 'rebirth' (Jezierski et al., 1999). The last true wild horse - *E. ferus przewalskii* was last time observed in Gobi desert in 1969 and it survived only thanks to capturing of small number of individuals, which were and are bred in captivity and recently they have been reintroduced to Mongolian steppes (for details see Robovský, 2009). If we take into account the feral horses, *i.e*. descendants of domestic horses living in the wild again (McKnight, 1959), the situation is different. Nowadays feral horses live again in North (Berger, 1977; Beschta et al., 2013; Girard et al., 2013) and even in South America (Pacheco and Herrera, 1997), appeared in some places in Europe (Tyler, 1972; Linklater, 2000) as well as in Asia (e.g. Khalil and Kaseda, 1997) and they were carried to Australia and New Zealand (Linklater et al., 2000; Hampson et al., 2010; Kampmann et al., 2013). Their population are described from the equator to the temperate-boreal frontier, in deserts and high-rainfall regions, and at low altitudes on river deltas and islands or in the high-altitude mountainous regions of central continents (Linklater, 2000).

1.2. SOCIAL ORGANIZATION OF 'WILD' HORSES

'Running wild through continents with the band of fellows - lost but not forgotten past.'

The basic unit of feral horse society is the band composed of the adult stallion(s) and several mares with their offspring, so-called harem (Tyler, 1972; Berger, 1977; Salter and Hudson, 1982; McCort, 1984; Kaseda et al., 1995; Linklater et al., 2000; Cameron et al., 2003). However using this term is a bit questionable because of changes of female members during time (for details see Tyler, 1972; Linklater, 2000). Moreover some authors sometimes separate harems and a multi-stallion bands (McCort, 1984), groups with at least 2 stallions up to number of 5 (Salter and Hudson, 1982; Linklater, 2000; Linklater et al., 2000). These multi-stallion bands are unique in organization. All stallions usually cooperate with each other in warding off the intruders (solitary stallions) (Salter and Hudson, 1982; McCort, 1984), but one of them is always dominant over the others and he still keeps the paternity of most foals (Bowling and Touchberry, 1990; Asa, 1999). But this situation causes the need of creation of a dominance hierarchy similar to mares' (Salter and Hudson, 1982). The advantages of this multi-stallion cooperation for both the stallions and mares are disputable (Linklater and Cameron, 2000; Cameron et al., 2003). It is more likely a mate parasitism than formerly supposed mutualism or reciprocal altruism between stallions (Linklater and Cameron, 2000). The mares from this type of bands were found out more protective of their foals, particularly when stallions and foals approached one another because of proved infanticide in horses (Duncan, 1982; Ryder and Massena, 1988).

The harem size range from 2 to 35 members including stallion(s) (Tyler, 1972; Berger, 1977; Salter and Hudson, 1982; Kaseda and Khalil, 1996; Pacheco and Herrera, 1997), and it depends mostly on the environment, resources distribution and possible human disturbance and restrictions which has been reported in literature (reviewed in McCort, 1984; Linklater, 2000). Kaseda and Khalil (1996) reported also the other factor influencing the size of the harem - reproductive success. They suggested that reproduction success of harem stallion (the dominant one) is about 85%, *i.e.* he is a father of 85% of the foals in his harem, which had also been reported by Miller (1981). So if the dominant stallion monopolizes too many mares, he could not sire so many offspring because he could not always prevent his rival stallions from mating with his mares in wild or feral circumstances (Kaseda and Khalil, 1996). Maybe that's why he warns the intruder stallions about his presence using scent marking with faeces or less urine which is centred around communal faecal piles (Berger, 1977; Salter and Hudson, 1982).

Particular harems occupy non-exclusive home ranges throughout the year (Berger, 1977) which can often overlapped one another (Berger, 1977; Salter and Hudson, 1982; McCort, 1984). The size of the home range is also in relation to the environment, demography and population density. Thus when the forage and water resources are poor or scattered and unpredictable in availability the home range size is quite large (e.g. in

Red Desert in Wyoming where the size ranges from 78 to 303km2 (Miller, 1983)). On the other hand in the environment abundant in resources the home range size are usually small as well as in small area regions, *i.e*. islands or human restricted areas (Rubenstein, 1981; Linklater et al., 2000). In such a small places like islands are it can be observed even 'territories' creation, e.g. on Shackleford Banks island in North Carolina coast (Rubenstein, 1981).

The harems are relatively stable in their composition (Salter and Hudson, 1982; Linklater, 2000). This stability can be explained with major reproductive advantage (higher foaling rates and shorter delivery intervals) for mares which maintain long-term and stable consort relations with a particular stallion throughout their reproductive life span (Kaseda et al., 1995). The only changes in composition occurred when the young animals of both sexes leave their parental bands (Salter and Hudson, 1982; Kaseda et al., 1984; Feh, 1990), effectively preventing breeding between a male and his female offspring (avoid inbreeding (Monard and Duncan, 1996)) resulting (usually) in the separation of siblings (Salter and Hudson, 1982). After leaving, the young males can remain solitary or they can form an unstable associations of young males so-called bachelor groups and they can stay in these herds for several years as long as they form their own harems (Tyler, 1972; Rubenstein, 1981; McCort, 1984; Kaseda et al., 1997; Pacheco and Herrera, 1997); nevertheless not all of them succeed (Salter and Hudson, 1982; Kaseda et al., 1997). The young females are usually integrated into other stallion's harem or they can be a wandering mares of both types solitary or grouped for a while (Pacheco and Herrera, 1997; Khalil and Murakami, 1999). The young animals of both sexes leave their natal bands before they reach sexual maturity at the age of 1-4 years (Tyler, 1972; Kaseda et al., 1984). Usually the separation is permanent from the beginning, but several returning and repeated separations shortly after 'first' one sometimes occurred (Tyler, 1972). Time of leaving also depends on several factors - birth of a new sibling, mother’s death, forage availability etc. (Tyler, 1972; Kaseda et al., 1984; Monard and Duncan, 1996; Kaseda et al., 1997). Females usually leave their natal band voluntarily (Kaseda et al., 1984; Monard et al., 1996; Stanley and Shultz, 2012) and usually around their oestrous because they are sexually attracted to unfamiliar males (*i.e*. from outside the natal group) (Monard et al., 1996). On the other hand although males usually leave their natal band voluntarily too

(Tyler, 1972; Kaseda et al., 1984; McCort, 1984), sometimes they can be driven away by dominant male(s) after reaching sexual maturity (Tyler, 1972; McCort, 1984); especially if they stay in natal band too long probably because of taking advantage of prolonged safety and social learning necessary to become a successful breeding stallion (Stanley and Shultz, 2012).

When looking deeper into horses' organization to intra-band relationships, we ascertain that both feral (Tyler, 1972; Berger, 1977; Keiper and Sambraus, 1986) and domestic horses (Van Dierendonck et al., 1995; Weeks et al., 2000; Heitor and Vicente, 2010a) establish a dominance hierarchy within band. These dominance hierarchies are usually relatively stable (Berger, 1977; Houpt and Wolski, 1980) with exception of dispersal of sub adult horses or deaths of some individuals and on the other hand coming of new sub adult mares (e.g. Tyler, 1972). Mares generally form linear hierarchies in smaller breeding groups (Tyler, 1972; Heitor et al., 2006; Vervaecke et al., 2007) but in larger ones it can be triangular or more complex (Houpt et al., 1978). Bachelor groups have more unstable (McDonnell and Haviland, 1995; Heitor and Vicente, 2010b), but also linear hierarchy (Feh, 1988; Tilson et al., 1988; Vervaecke et al., 2007) in relation to comparatively frequent changes in their composition, as the stallions integrate into or leave them, and fighting among stallions to achieve social skills necessary for establishing their own harems (Berger, 1986; McDonnell and Haviland, 1995; Khalil and Kaseda, 1998). Harem stallions may or may not be dominant over mares (Berger, 1977; Houpt and Keiper, 1982; Keiper and Sambraus, 1986; Boyd, 1991). The position of individual in dominance hierarchy depends on many factors whose influence is discussed in literature. Most often mentioned factors are: individual's aggression level (Tyler, 1972; Houpt et al., 1978; Araba and Crowell-Davis, 1994; Weeks et al., 2000), age (Houpt and Keiper, 1982; Keiper and Sambraus, 1986; Van Dierendonck et al., 1995; Sigurjonsdottir et al., 2003; Van Dierendonck et al., 2004; Heitor and Vicente, 2010a), weight or height (Houpt et al., 1978; Rutberg and Greenberg, 1990; Van Dierendonck et al., 1995), length of residency in the herd (Van Dierendonck et al., 1995; Heitor et al., 2006), foaling status (Keiper and Sambraus, 1986; Heitor and Vicente, 2010a), maternal dominance position (e.g. Houpt et al., 1978; Houpt and Wolski, 1980; Araba and Crowell-Davis, 1994; Weeks et al., 2000) or age at castration for geldings (Van Dierendonck et al., 1995).

In conclusion, feral horses live in relatively unchanging spatial and social organization resembling their ancestral pre-domestic conditions which persist through variable environmental and demographic characteristics (Linklater, 2000). Genetic variability of the feral populations of horses is maintained by dispersing of the young animals of both sexes from their natal bands. Thus the level of inbreeding in feral population stay low (Duncan et al., 1984a) maintained especially by females because they usually accepted mating only with males of other groups in spite of frequent sexual approaches by males of their natal groups (normally close relatives) in oestrous (Monard et al., 1996). Also their mothers share this avoiding as they interposed themselves when close kin males of the natal group approached their daughters sexually (Monard et al., 1996). Generally reducing sexual activity with the members of natal band (*i.e.* in filly-harem stallion, brother-sister, mother-son pairs) based on experience is also probable the mechanism which led to the reduction of inbreeding (Duncan et al., 1984a). On the other hand domestic horses are often exposed to a situation when mated with their close kin for the purpose of maintaining specific breed features. Moreover this process may result in high level of inbreeding which has been found to have different negative effects on reproductive traits in many species, including horses (for details see below).

1.3. REPRODUCTION VS. INBREEDING

'In pursuit of viable and quality progeny wild horse wins – human failed.'

Although the world is currently populated with quite great number of domestic horses, they are scattered into almost 1000 separated breeds (Cieslak et al., 2010), which are usually closed for breeding one another. It has been reported that populations with reduced genetic variability often experience reduced growth and increased extinction rates (Lacy, 1997; Brook et al., 2002; Keller and Waller, 2002). If so, the problem of too small numbers of horses of individual breeds needed for maintaining their genetic variability large enough was revealed.

Small populations lose genetic variability because of genetic drift (Lacy, 1997; Keller and Waller, 2002). In addition the inbreeding within populations can further decrease individual variability which can strongly affect both individual and population viability through depressing e.g. resistance to diseases, parasites and predation, and flexibility in coping with environmental challenges (e.g. Lacy, 1997; Keller and Waller, 2002). Moreover, close inbreeding has been known for 'centuries' to bring about a reduction of offspring as well as adults fitness (Lacy, 1997; Keller and Waller, 2002; Kristensen and Sorensen, 2005) which can be caused by a number of genetic factors (Crnokrak and Roff, 1999): the unmasking of recessive deleterious alleles (Lande, 1994; Lynch et al., 1995), increased homozygosity (Keller and Waller, 2002) and/or reduced allozyme variability (Pray et al., 1994). Thus higher risk of population extinction can be expected in small populations where the depletion of genetic variability will slow adaptive evolution and the genetic drift can lead to accumulation of maladaptive traits (Lacy, 1997). The impacts of these processes would be seen in reduced ability to survive in present environments and to adapt to new ones, and thus would be intertwined with non-genetic traits (Lacy, 1997).

Inbreeding, *i.e*. mating of related individuals, has been observed to have a negative influence on many fitness-related features in various species (Lacy, 1997), e.g. juvenile mortality (Ralls et al., 1979; Uzmay and Akbas, 2003; Mandal et al., 2004), litter size or amount of progeny (Rodriganez et al., 1998; Fredrickson et al., 2007; Haanes et al., 2013; Cain et al., 2014), growth or body size (Mandal et al., 2002; Nielsen et al., 2012; Brzeski et al., 2014; Eteqadi et al., 2014; Fareed and Afzal, 2014; Mokhtari et al., 2014), susceptibility to diseases or parasite infestation (Rudan, 1999; Valsecchi et al., 2004; Acevedo-Whitehouse et al., 2005; Charpentier et al., 2008b; Brambilla et al., 2015), male reproductive success through sperms in general (Wildt et al., 1982; Wildt et al., 1987; Gomendio et al., 2000; Van Eldik et al., 2006; Asa et al., 2007) etc. The variety of impacts on fitness is called inbreeding depression (Lacy, 1997). The complexity of the inbreeding effects on fitness traits reside in varying across taxa, populations and environments (Keller and Waller, 2002; Kristensen and Sorensen, 2005). Thus population may suffer from inbreeding depression in one environment but not in another (Pray et al., 1994). Likewise, inbreeding does not affect all traits to the same degree (fitness vs. non-fitness traits) and besides traits affected by inbreeding may mutually interact in reducing overall fitness (Kristensen and Sorensen, 2005). It follows that the impact of inbreeding also differs between natural and captive conditions (Ralls et al., 1988; Jimenez et al., 1994; Crnokrak and Roff, 1999).

Not many studies of inbreeding depression in wild populations from natural habitats exist (e.g. Coltman et al., 1998; Amos et al., 2001; Bean et al., 2004) in comparison with the numbers of that done in captive populations (e.g. Ralls et al., 1979; Wang et al., 2001; Mandal et al., 2004; Cassinello, 2005; Adamec et al., 2006; Van Eldik et al., 2006). On one hand most probably because of the problems with acquiring the pedigrees of wild populations and on the other hand because of the economy costs of genotyping for quite large quantity of microsatellite marker loci (100 or more) when calculating inbreeding via genetic analyses (Baumung and Solkner, 2003). Inbred wild and/or reintroduced species measured under natural conditions had a substantially higher mean cost of inbreeding especially in fitness traits such as juvenile mortality (Jimenez et al., 1994; Crnokrak and Roff, 1999). First the juveniles may die as a result of unpredictable environmental factors, such as predation, weather extremes, and food stress or epidemic diseases (Jimenez et al., 1994; Crnokrak and Roff, 1999). Secondly many weak young that would normally die in the wild would most likely survive in captivity with veterinary assistance (Ralls et al., 1988). Furthermore, even when we do not prove the inbreeding effects in natural populations it does not mean that they do not exist (Crnokrak and Roff, 1999). The two most commonly suggested reasons why inbreeding effects in natural populations may not be significant are: i) animals in the wild avoid close inbreeding (e.g see mechanism of natal dispersal in feral horses (Duncan et al., 1984a)), and therefore do not manifest the deleterious fitness effects; and ii) even if inbreeding does occur, animals are able, either behaviourally or physiologically, to deal with the deleterious genetic effects before they are manifested on a phenotypic level, whereas captive species, because of the conditions of captivity, cannot respond in such a manner (Crnokrak and Roff, 1999).

Anyway Lacy (1997) concluded that no species of mammal has been shown to be unaffected by inbreeding, so we can suppose that a horse, feral or captive, is not an exception. As is mentioned above feral horse populations are more affected by environment conditions and because of that their foaling rates have quite large range from 30 to 80% (Berger, 1986; Siniff et al., 1986; Garrott, 1991; Scorolli and Lopez Cazorla, 2010; Dawson and Hone, 2012) depending also on the age of the females; foaling rates increase as mare matures (Linklater et al., 2004). Also their juvenile survival rates varied greatly - from 12% to 97% (Berger, 1986; Siniff et al., 1986; Garrott and Taylor, 1990; Greger and Romney, 1999; Linklater et al., 2004; Scorolli and Lopez Cazorla, 2010). However, no studies which prove the inbreeding effects on feral horses' foaling rates or juvenile mortality exist.

When we focused on captive horse's reproduction we ascertain that humans commonly use preferential mating of relatives for improving desirable heritable traits and for maintaining them in many breeding programs of captive animals such as horses (Kristensen and Sorensen, 2005). So many breeds of horses are more or less inbred (e.g. Valera et al., 2005; Cervantes et al., 2008; Sairanen et al., 2009; Bhatnagar et al., 2011; Vostry et al., 2011; Binns et al., 2012) and this can be reflected on their reproductive success, *i.e.* on juvenile mortality, fertility including pregnancy failures, or sperm quality (Klemetsdal and Johnson, 1989; Sevinga et al., 2004; Van Eldik et al., 2006). The captive horses' foaling rates are similar to feral ones reaching values around 70-80% (e.g. Hevia et al., 1994; Morris and Allen, 2002), but without such large ranges. This is probably caused by minimized environmental influences such as predation, weather extremes or food stress. On the other hand captive horse reproduction has its own problems because of human restrictions, which usually disrupt natural course of mating (for details see Asa, 1986;

McDonnell, 2000; Crowell-Davis, 2007) or because of using assisted reproductive techniques such as insemination, introcytoplasmic sperm injection or embryo/oocyte/nuclear (*i.e.* cloning) transfer (Aurich and Aurich, 2006; Vanderwall, 2008). Moreover fertility or fecundity of captive horses can be influenced also by inbreeding of mother, father or their potential offspring (Klemetsdal and Johnson, 1989; Sevinga et al., 2004).

Finally, we have to mention that not only inbreeding can cause pregnancy failures such as early embryonic loss or abortion, or other failures such as stillbirth, dystocia (*i.e.* difficult delivery) or neonatal death. Wide range of causes of these failures has been described in literature (e.g. Smith et al., 2003; Jonker, 2004; Karadjole et al., 2008; Vanderwall, 2008; Bartos et al., 2011; Marenzoni et al., 2013). Vanderwall (2008) use three categories of factors that may contribute to the occurrence of embryonic loss in the mare. Intrinsic factors are those which are related to mother, e.g. endometrial disease, progesterone insufficiency, maternal age, maternal chromosomal abnormalities etc. Extrinsic factors include stress, nutrition, season or climate, sire, semen or gamete processing/handling etc. Embryonic factors include chromosomal abnormalities or other inherent embryo characteristics. Additional sorting of causes of foetal deaths is determined in the review of Jonker (2004). Infectious causes include bacteria, viruses or fungi that are species specific or not; and non-infectious causes include manifold problems with umbilical cord or placenta. Since the inbreeding may affect some of these factors (e.g. through lowered resistance to some diseases as was described above), it may affects these failures indirectly. However the true cause of pregnancy failures or neonatal deaths often remains unknown (Smith et al., 2003).

1.4. MOTHER-OFFSPRING TRADE OFF

'When invested more and when stop the investment into offspring? – that's the question.'

In continuity of mating with stallion, mare usually conceives and commonly gives birth to one offspring. The twinning in horses is quite rare as it terminates in most cases in abortion, stillbirth, perinatal losses, or delivery of dead, weak or unviable deformed foals (Meier et al., 1997; Zoldag et al., 2001).

We can divide the maternal investment into offspring to two periods ending with weaning the offspring (this part is described in chapter below). First one - the gestation period - starts with conception and continues up to parturition lasting about 11 months, but it ranges from 312 to 409 days as reported in literature (Dos Santos Dias et al., 1998; Davies Morel et al., 2002; Perez et al., 2003; Heidler et al., 2004; Valente et al., 2006; Valera et al., 2006; Crowell-Davis, 2007; Winter et al., 2007; Bene et al., 2013). The length of gestation can be influenced with environmental (e.g. climate, photoperiod), foetal (e.g. sex of foetus), maternal (e.g. breed, age, parity or nutrition) and other factors (male effect) (reviewed in Satue et al., 2011).

The second period - lactation - starts immediately after foaling and lasts up to the weaning of the foal. Among mammals, lactation is the most energy demanding part of parental care (Pond, 1977; Oftedal, 2000) causing occurrence of many adaptations of the physiology and anatomy of the mother in pursuit of the best possible support to the offspring (Pond, 1977; Oftedal, 2000; Heidler et al., 2004; Filipovic et al., 2010). It follows expected parent-offspring conflict that parent (mother) and offspring should disagree over how long the period of the parental investment should last and over the amount of parental investment that should be provided (Trivers, 1974). Simply there comes a time during lactation when a mother will improve her reproductive success by weaning her young and investing resources in the next pregnancy (Duncan et al., 1984b). Conflict arises because the young wants continuous investment by the mother which would increase its own chances of survival and reproduction (Duncan et al., 1984b), especially in male foals (Stanley and Shultz, 2012).

Sex differences in suckling behaviour have been recorded in various ungulates (reviewed e.g. in Hewison and Gaillard, 1999) including equids, *i.e.* horses (Duncan et al., 1984b; Cameron and Linklater, 2000) and zebras (Pluhacek et al., 2011). In horses it was found out by Duncan et al. (1984b) that male foals spent more time suckling in the first 8 weeks of their lives than females. They suggested this higher effort in suckling interest by male foals due to their increased activity and lower time spent with feeding, compared to females. Although it has been reported that time spent suckling (suckling bout duration) do not adequately predict milk intake by the foal (Cameron et al., 1999b), the possible extra milk gained by colts can be apparently used, partly or wholly, to allow them spend more time active (Duncan et al., 1984b). An important component of this male activity is play (Duncan et al., 1984b) which is energetically costly and accounts for the major part of the exercise taken by foals (Fagen and George, 1977). Inasmuch as the fighting among equids in general, depends less on weight than on speed and agility (Berger, 1981), it is important especially for male foals to train their musculoskeletal system, through play and locomotion activities, and their physical proficiency (Kurvers et al., 2006). Consequently, if extra maternal investment enables foals to play (do exercise) more in first months of life (Cherdchutham et al., 2001) and in adolescence (e.g. Rogers et al., 2005), musculoskeletal development may be enhanced, as well as social development

(Cameron et al., 2008). Thus this fact helps the youngsters to improve their 'fighting' and social abilities enabling them increase their reproductive success later since this improvement endures into adulthood (Back et al., 1995; Santamaria et al., 2004). In the background of horse social organization (for details see chapter 1.2. above) where males have more variable reproductive success than females (Feh, 1990), mother may bias her investment according to the sex of the offspring and her own body condition (Trivers and Willard, 1973). Thus individual mothers (mares) invested more in their sons in terms of maternal care patterns, costs to maternal body condition and costs to future reproduction when they are in good condition and in daughters when they are in poor condition (Cameron and Linklater, 2000).

In equids post-partum mares experience oestrus, commonly called 'foal heat', during the first week after birth and may conceive at this time (Tyler, 1972; Boyd, 1991; Crowell-Davis, 2007). This situation further intensifies mother-offspring conflict due to concurrent pregnancy and intensive lactation as it has been reported that pregnant mares weaned their foals earlier than non-pregnant ones (Duncan et al., 1984b; Cameron et al., 2000) even in captivity under optimal nutrition (Pluhacek et al., 2007). Recently there has been also found shorter suckling bouts in pregnant captive plain zebra mares than in non-pregnant ones (Pluhacek et al., 2010a).

It was mentioned above that time spent suckling do not adequately predict milk intake by the foal (Cameron et al., 1999b). Thus nowadays the most of studies assessed suckling in equids through an inverse measure of maternal care using variables attesting about mother willingness to provide care, *i.e.* termination of suckling bouts by mother, maternal rejection during suckling bouts or foal's suckling attempts (Heitor and Vicente, 2008; Pluhacek et al., 2010c). Mainly it is mother who can influence suckling duration and frequency or rejection, and the way of its termination (Tyler, 1972; Duncan et al., 1984b). While the foal initiate the vast majority of nursing bouts (Tyler, 1972; Carson and Woodgush, 1983a; Crowell-Davis, 1985; Barber and Crowell-Davis, 1994). It has been reported that the mother play an active role in regulating duration of suckling bouts both early and late lactation, but for the greater part of it, the foals voluntarily terminated almost all bouts (Duncan et al., 1984b; Crowell-Davis, 1985; Barber and Crowell-Davis, 1994). The mothers terminated the suckling bouts mainly by moving off (90%) and partly by kicking their ventral abdomen (4%) or lifting a hind limb into the way (4%) (Duncan et al., 1984b; Crowell-Davis, 1985). An aggressive terminations are rare (2%), however in the final stage of lactation, at weaning, are more common and mother again terminates a large proportion of bouts (42%) (Duncan et al., 1984b; Crowell-Davis, 1985). Moreover the suckling itself is greatly influenced with individual maternal style or abilities (Crowell-Davis, 1986; Cameron and Linklater, 2000). Individual mothers can invest in lactation differently according to their maternal experiences (Duncan et al., 1984b; Cameron et al., 2000), age (Cameron et al., 2000), condition (Cameron et al., 1999a; Cameron and Linklater, 2000), species or breed (Martuzzi et al., 2004), pregnancy and foetus sex (Duncan et al., 1984b; Pluhacek et al., 2007) or position in social hierarchy (Feh, 1990; Heitor and Vicente, 2008).

Finally, because equid mares, both feral and captive, form social hierarchies (Tyler, 1972; Berger, 1977; Lloyd and Rasa, 1989; Van Dierendonck et al., 1995; Weeks et al., 2000; Pluhacek et al., 2006), suckling bouts can be actively terminated by herdmates, who are dominant over the foal's mother, with biting and threats (Tyler, 1972; Rutberg and Greenberg, 1990; Pluhacek et al., 2010c). This may cause lower condition in submissive than dominant mares' foals (Tyler, 1972; Pluhacek et al., 2006).

It seems that foals of both sexes can benefit from their mother's dominance rank and they might become dominant in adulthood (Houpt et al., 1978; Feh, 1990; Araba and Crowell-Davis, 1994; Monard and Duncan, 1996; Sigurjonsdottir et al., 2003). Nevertheless whether the predisposition to dominant or submissive position is learned or somehow 'inherited' is unclear (Houpt and Wolski, 1980; Araba and Crowell-Davis, 1994). On one hand mother can actively defend their foal against other subordinate herdmates, both adults and foals, which might create association of submission also towards her offspring (Tyler, 1972). On the other hand foal can learn association of mother's behavioural patterns towards individual horses and it can repeat them (Tyler, 1972; Araba and Crowell-Davis, 1994; Weeks et al., 2000).

1.5. WEANING

'If we know that weaning offspring abruptly from mothers costs so much, why we do this?'

Weaning is a time when foal is passing through invisible border between 'to be a defenceless foal' and 'to be a sub adult self-sufficient horse'. However natural and forced (*i.e.* under human management) weaning differs considerably in many features which are described below.

Natural weaning in equids is a gradual process that starts at about 8 months of age and its termination depends mostly on the mare's body condition and her reproductive status (Tyler, 1972; Carson and Woodgush, 1983b; Duncan et al., 1984b; Berger, 1986; Cameron et al., 2000; Pluhacek et al., 2007). In connection with these two facts pregnant mares usually wean their foals before one year of age, *i.e*. in the winter before the next spring delivery, but sometimes they suckle the foal up to few weeks or only days before parturition (Tyler, 1972; Duncan et al., 1984b). On the other hand mares who failed to conceive in a subsequent season may continue to nurse their yearlings up to two years of age or longer (Tyler, 1972; Duncan et al., 1984b). The positive fact of the natural weaning is that cessation of milk support does not usually break the mother-offspring bond and does not cause a radical social or environmental changes for the foal who continue to stay close to mother and in its natal band (Tyler, 1972; Monard et al., 1996). Feral mares usually wean their foals using threatening or avoiding them whenever they approached them to suck and around parturition they even bite or kick them out to specific individual range, but after few days they allowed the older foals to remain in closer proximity to them and their new foal and to maintain the bond by grooming or using them as 'refuge' in jeopardy (Tyler, 1972). Thus mother-offspring bond can persists for several years not only in many mammalian species as it is reviewed in Newberry and Swanson (2008) but also in horses where it remains strong until the foal leaves the natal group at the age from 1 to 4 years (Tyler, 1972; Monard et al., 1996; Khalil and Kaseda, 1997).

In contrast, weaning under human management is one of the most stressful events in the foal's life with possible long-lasting consequences for both mother and foal (Houpt et al., 1984; McCall et al., 1985; McCall et al., 1987; Apter and Householder, 1996; Heleski et al., 2002; Waran et al., 2008; Erber et al., 2012; Henry et al., 2012). There are a few differences compared to natural one. Time of weaning is considerably put off closer towards the birth. In common practice, weaning of foals usually occurs at the age of four to eight months (McCall et al., 1985; Weeks et al., 2000; Heleski et al., 2002; Rogers et al., 2004; Ladewig et al., 2005). Time of weaning on horse farms usually reflects the trade-off between two opposite concerns of the breeders. First deep-rooted concerns about the condition of the mare resulting in earlier weaning (Apter and Householder, 1996; Ladewig et al., 2005) which seemed to be baseless as we mentioned; mares, if they are allowed to, weaned their foals dependently on their own condition (Tyler, 1972; Carson and Woodgush, 1983b; Duncan et al., 1984b; Berger, 1986; Cameron et al., 2000; Pluhacek et al., 2007). However, it is not known how mares allocate resources between foal and foetus depending on their condition. Secondly concerns about the developmental and behavioural impact of the weaning on the foal resulting in a tendency to delay weaning.

The most widespread practice is abrupt weaning where the mare and foal are suddenly and completely separated by distance to prevent them to see, hear or smell each other (McCall et al., 1985; Apter and Householder, 1996; Ladewig et al., 2005). Besides nutritional changes (loss of milk), foals born to domestic horses usually experienced multiple cumulative changes at artificial weaning, *i.e*. loss of the mother and change of the physical and social environment (Apter and Householder, 1996; Nicol et al., 2005; Newberry and Swanson, 2008; Waran et al., 2008). It is supposed that these changes can be a source of stress in foals (reviewed e.g. in Waran et al., 2008). Stress affects normal biological functions of the animals through biological responses that are used to solve stressful situation (Moberg, 1987; Morgan and Tromborg, 2007). Thus in stressful period resources (energy) are allocated to the activities assisting the animal to cope with stress (Moberg, 1987; Morgan and Tromborg, 2007), such as increased vocalization, locomotion or stereotypic or self-destructive behaviour (e.g. Houpt and Hintz, 1983; McGee and Smith, 2004; Nicol and Badnell-Waters, 2005; Berger et al., 2013), increased heart rate and respiration, or increased secretion of various isomers of adrenal glucocorticoids, and therefore they are unavailable for biological needs (Moberg, 1987; Morgan and Tromborg, 2007). Growth rate disruption or body weight reduction as a consequence of the stress has been documented across quite different species from Atlantic salmon juveniles (McCormick et al., 1998), through rats (Konkle et al., 2003) and laboratory mice (Bartolomucci et al., 2004) to domestic pigs (Hemsworth et al., 1981). So when speaking of growth disruptions that usually occur immediately after weaning not only in horses (Houpt et al., 1984; Griffin et al., 1995; Warren et al., 1998; Rogers et al., 2004) but also in other domestic species like cattle (Price et al., 2003; Sweeney et al., 2010) or pigs (McCracken et al., 1995; Hoetzel et al., 2011), we cannot forget to mention increase incidence of health problems, in horses e.g. Developmental Orthopaedic disease (Donabedian et al., 2006; Lepeule et al., 2009).

Evaluation of stress in foals has been thereafter based on various indicators, mentioned above, such as foals' behaviour (Heleski et al., 2002; Henry et al., 2012); activity (McCall et al., 1985); cortisol levels (or levels of other metabolites) from blood (McCall et al., 1987; Malinowski et al., 1990; Hoffman et al., 1995) or saliva samples (Moons et al., 2005; Erber et al., 2012); growth rates (Warren et al., 1998; Coleman et al., 1999); or trainability, tractability or novel object responses of the foals (Nicol et al., 2005).

Despite considerable repercussions described above, abrupt weaning, is still commonly imposed, not only in horse farms, as a more feasible and cost-effective practice (Apter and Householder, 1996). However various alternative methods that may helped offspring to cope with artificial weaning have been subjected to detailed research (reviewed in Apter and Householder, 1996; Newberry and Swanson, 2008; Waran et al., 2008; Enriquez et al., 2011). These more natural-like weaning techniques, which appear to be associated with lower levels of stress in both mother and foal, can be divided into a few groups. First group works with various gradual techniques of mother-offspring separation; e.g. training short-term isolation from the mother before permanent separation (Orgeur et al., 1998; Moons et al., 2005; Simitzis et al., 2012); gradual removal of mares from the herd (Rogers et al., 2004; Erber et al., 2012); partial separation allowing fence-line contact with mother (McCall et al., 1985; Church and Hudson, 1999; Price et al., 2003; Enriquez et al., 2010); or prevention of suckling shortly before mother’s removal (Haley et al., 2005; Schichowski et al., 2008; Enriquez et al., 2010). Second group uses one or more companions to reduce the stress at weaning; e.g. weaning offspring in pairs (Houpt et al., 1984; Malinowski et al., 1990; Hoffman et al., 1995; Villeneuve et al., 2009) or groups (Heleski et al., 2002); or presence of some unrelated adult(s) in the herds of weaned young (Henry et al., 2012). Third group applies feeding different diets around weaning (McCall et al., 1985; Hoffman et al., 1995; Coleman et al., 1999; Nicol et al., 2005) which can affect activity and reactivity of the young (Holland et al., 1996) and reduce stress (Jose Redondo et al., 2009). Fourth group tries to enrich the environment of separated (weaned) offspring allowing them to graze in paddock (e.g. Heleski et al., 2002) or using novel visual item (Budzynska and Krupa, 2012). The last group manipulates changes (change of social group or environment, moving etc.) following weaning; e.g. leaving weanlings in home environment for some time (Ekkel et al., 1995; Puppe et al., 1997; Nicol et al., 2005; Hoetzel et al., 2011; Lynch et al., 2011); but they generally do not take later removal of the 'home-weaned' offspring into account.

While the consequences of weaning are well documented in foals, there are not many studies in mares except of the research of Malinowski et al. (1990) who found out high level of plasma cortisol and reduced cell-mediated immune response in mares whose foals were weaned in pairs. This fact may unlock the further direction of research in this field.

1.6. BEHAVIOUR PATTERNS IN JEOPARDY BECAUSE OF INBREEDING

'My mom is my half-sister, my dad is my grandfather – is that why do I behave strangely..?'

Inbreeding, *i.e*. mating of related individuals, redistribute the frequency of genotypes, increasing the proportion of homozygotes and correspondingly decreasing the proportion of heterozygotes in the population and thus causes inbreeding depression (Keller and Waller, 2002; Charlesworth and Willis, 2009). It is generally considered that inbreeding depression is primarily due to the expression of deleterious alleles rather than overdominance (Charlesworth and Charlesworth, 1987; Charlesworth and Charlesworth, 1999; Roff, 2002; Charlesworth and Willis, 2009). Furthermore, the life history traits have greater directional dominance (*i.e*. they are affected by a larger number of single traits and thus a larger number of loci) and hence should show greater inbreeding depression than morphological traits (Crnokrak and Roff, 1995; DeRose and Roff, 1999; Wright et al., 2008).

It was mentioned above (see part 1.3. for details) that inbreeding lowers fitness-related characters in many species of animals, including humans (e.g. reviewed in Jimenez et al., 1994; Keller and Waller, 2002; Kristensen and Sorensen, 2005; Charlesworth and Willis, 2009). In comparison with that, relatively little is known about the effects of inbreeding on patterns of animal behaviour, be it maternal/paternal, sexual, social or other.

In some of both invertebrate and vertebrate species was confirmed a detrimental effect of inbreeding on behaviour, which can lower the reproduction success. They are: 1) mating/sexual behaviour, e.g. in male crickets (*Teleogryllus commodus*) (Drayton et al., 2011), freshwater snails (*Physa acuta*) (Janicke et al., 2014), guppies (*Poecilia reticulata*) (Mariette et al., 2006), killifish (*Heterandria formosa*) (Ala-Honkola et al., 2009), 2) aggression levels and competitive ability, e.g. in salmonid fish (Tiira et al., 2003; Gallardo and Neira, 2005), house mice (*Mus domesticus*) (Eklund, 1996), common shrews (*Sorex araneus*) (Välimäki et al., 2007), rhesus macaques (*Macaca mulatta*) (Charpentier et al., 2008a), 3) activity e.g. in oldfield mice (P*eromyscus polionotus*) (Margulis, 1997), 4) social behaviour e.g. in rhesus macaques (*Macaca mulatta*) (Charpentier et al., 2008a).

Although higher dominance positions within hierarchies (*i.e*. social success) are believed to be connected to better condition and higher reproductive success in mammals (Cassinello and Alados, 1996; Pusey et al., 1997; Weeks et al., 2000; Pluhacek et al., 2006), the connection between inbreeding and social success has a negligible attention through literature (see above). The one study made by Charpentier et al. (2008a) showed that female rhesus macaques with lower mean heterozygosity received higher rates of aggression and lower rates of affiliation from non-kin than more heterozygous females. On the other hand neither the acquisition of alpha status in males, nor social in females was influenced by the individual's heterozygosity in mandrills (*Mandrillus sphinx*) (Charpentier et al., 2005).

Finally, inbreeding can influence the social behaviour or success (*i.e*. dominance position) in mammals simply by changing some part of behaviour pattern, like aggressiveness etc. (Charpentier et al., 2008a), or by influencing a morphological features (in horses e.g. Bergmann et al., 1997; Gomez et al., 2009), which can be responsible for social success like weight (in horses e.g. Ellard and Crowell-Davis, 1989, for details see part 1.2.). Furthermore, the domesticated animals, including horses, where the probability of inbreeding is quite high, are a good subject for studying the relationship of inbreeding and behaviour. However, the studies about this issue are quite rare or wholly missing, like at horses. So further research in this field is needed.

2. AIMS OF THE THESIS

The aim of the thesis was to address following issues in social behaviour and reproduction of domestic horses under human management: high inbreeding, social success, suckling in limited space, mother-offspring conflict and weaning stress. A set of questions covering three key periods of foal's life, follows in a chronological order from conception to weaning, threads here with questions about obtaining the dominance position and social skills. The results have so far resulted in six manuscripts.

AIM 1: DOMINANCE POSITION AND MATERNAL EFFECTS

QUESTION 1: MAY BE THE MATERNAL DOMINANCE POSITION, PLUS DIFFERENCES IN SUCKLING PARAMETERS OR MATERNAL STYLE RESPONSIBLE FOR LATER OUTCOME OF THE OFFSPRING DOMINANCE POSITION?

① Komárková, M., Bartošová, J., **Dubcová, J.**, (2014). Age and group residence but not maternal dominance affect dominance rank in young domestic horses. Journal of Animal Science. 92:5285-5292.

This study focused on factors influencing dominance position in young horses, with emphasis on the role of the mother in order to uncover the possible transference ('inheritance') of the dominance rank from the mother to the offspring, which still remains unclear.

AIM 2: MATING, PREGNANCY AND INBREEDING

QUESTION 2: ARE THE HIGHLY INBRED MARES LESS SUCCESSFUL IN OFFSPRING PRODUCTION?

② **Dubcová, J.**, Bartošová, J., (*in prep*). Lower reproductive success in highly inbred domestic horse mares: A message from 70 years of breeding history of an endangered population.

The research was focused on the reproductive success, such as pregnancy rate, foaling rate, new-born survival and foals' birth measures in relation to the level of inbreeding. The breeding management of small breeds endangered by low genetic variability should profit from this study.

AIM 3: MATERNAL CARE AND INVESTMENT

Question 3.1: How the pregnant mares, that nurse the foal, cope with double maternal investment?

(3.1) Bartošová, J., Komárková, M., **Dubcová, J.**, Bartoš, L., Pluháček, J., (2011). Concurrent lactation and pregnancy: pregnant domestic horse mares do not increase mother-offspring conflict during intensive lactation. PloS one, 6(8), e22068.

Our publication investigated double maternal investment during concurrent pregnancy and lactation and its potential displays in balanced nutritional conditions and zero predation. First aim of the study was to investigate the effects of pregnancy on suckling behaviour characteristics as indicators of mother-offspring conflict in domestic horses. The second aim was to acquire supporting arguments for later weaning of the foals and thus improving their welfare in present breeding managements.

Question 3.2: Are there any differences in maternal investment among mares, and if so, are they dependent on their dominance rank?

(3.2) Komárková, M., Bartošová, J., **Dubcová, J.**, (2011). Effect of mares' dominance rank on suckling behaviour in the loose housed domestic horses. Applied Animal Behaviour Science. 133, 54– 59.

This study focused on suckling period that is crucial for adequate physical, as well as psychical development of the foal. The aim of the study was to investigate if the dominance relationships and agonistic interactions among mares are responsible for differences in suckling behaviour which cannot be explained by the foal's age, under conditions characterized by balanced diet adjusted to the needs of lactating mares, but limited space.

AIM 4: WEANING, STRESS AND GROWTH

Question 4: Are there any differences in post-weaning growth in the foals based on weaning management?

④ **Dubcová, J.**, Bartošová, J., Komárková, M., (*in press*). Effects of Prompt vs. Stepwise Relocation to a Novel Environment on Foals' Responses to Weaning in Domestic Horses (Equus Caballus). Journal of Veterinary Behavior: Clinical Applications and Research.

The study focused on improving foals' welfare by reduction of stressful events immediately after abrupt weaning from the mother. Thus the aim was to investigate the impact of different time schedules of moving to a new environment after abrupt weaning on growth rate and saliva cortisol concentrations, as the stress indicators, in a group of loose-housed domestic horses.

AIM 5: INBREEDING VS. SOCIAL SUCCESS

QUESTION 5: ARE THE MORE INBRED HORSES LESS SUCCESSFUL IN OBTAINING THE SOCIAL SKILLS AND HIGHER DOMINANCE POSITION?

⑤ **Dubcová, J.**, Bartošová, J., Komárková, M., (*in prep*). Impact of Inbreeding on Social Behavior and Dominance Rank in an Inbred Population of Domestic Horses (*Equus caballus*).

This publication focuses on the potential detrimental effects of inbreeding on social behaviour of the domestic horses. The aim was to investigate if the inbreeding may influence the reaching higher dominance positions and initiation of agonistic as well as non-agonistic interactions by more inbred horses.

3· RESULTS AND DISCUSSION

AIM 1: DOMINANCE POSITION AND MATERNAL EFFECTS

① Komárková, M., Bartošová, J., **Dubcová, J.**, (2014). Age and group residence but not maternal dominance affect dominance rank in young domestic horses. Journal of Animal Science. 92:5285-5292.

In the first manuscript we investigated how the maternal characteristics and care underlie the foal's social dominance. We showed that foal age is the most important factor influencing their dominance position within the herd. Although the age as a factor influencing the dominance position was observed in many studies, the results of them are inconsistent. It remains unclear whether older horses always dominate the younger or, most likely, more factors play a role together (e.g. Tyler, 1972; Berger, 1977; Keiper and Sambraus, 1986; Araba and Crowell-Davis, 1994; Weeks et al., 2000). The advantage of early birth, compared to the other herdmates, persisted in our study up to age 3. The second factor which affected the dominance position of the foal was the length of residency within the group. This fact is in agreement with assumption known from literature that the dominance position of the horse is correlated to the length of residency within the herd (e.g. Van Dierendonck et al., 1995; Monard et al., 1996; Heitor et al., 2006). In conclusion, the most dominant horses in our study were mainly recruited from the first weaned group in a season, and they were also primarily the oldest individuals.

We did not confirmed the influence of maternal style or differences in suckling parameters (dominant mares nursed their foals longer and terminated fewer suckling bouts - as it shown in the fifth manuscript) on later outcome of the offspring’s dominance position. As in the study of (Heitor and Vicente, 2008) the dominance position of sub-adult offspring did not correlate to that of its mother, as had been reported in pre-weaned and post-weaned foals (Tyler, 1972; Wells and Goldschmidt-Rothschild, 1979; Weeks et al., 2000), as well as adult horses (Feh, 1990; Van Dierendonck et al., 1995; Monard and Duncan, 1996). Nevertheless, the foals born to the same mare in 2 consecutive seasons revealed fair repeatability in the dominance position they obtained at 3 years of age.

Our result referring to maternal influence on dominance position of the offspring indicate, that further research of the maternal style and its repeatability in horses is needed, because the data, either supportive or not (Crowell-Davis, 1986; Cameron and Linklater, 2000; Heitor and Vicente, 2008), is rare.

AIM 2: MATING, PREGNANCY AND INBREEDING

② **Dubcová, J.**, Bartošová, J., (*in prep*). Lower reproductive success in highly inbred domestic horse mares: A message from 70 years of breeding history of an endangered population.

In the second manuscript we investigated the possible effect of inbreeding level on reproduction-related traits in mares. The mares with extremely high inbreeding (more than 0.125) had lower foaling rates, *i.e*. the probability of delivery. Inbreeding level may thus negatively influence the overall fertility of the mares. This is in agreement with several previous studies, not only in horses (Cothran et al., 1984; Klemetsdal and Johnson, 1989; Langlois and Blouin, 2004; Sairanen et al., 2009; Langlois et al., 2012), but also in other species such as pigs (Kock et al., 2009), or livestock (Hinrichs and Thaller, 2011). The fertility of old mares was lower than the fertility of young or mid-age ones. The causes of the decreased fertility in older mares can be explained, first by a decrease in the quality of the oocytes produced by older mares, and second to a lesser extent by a deterioration in the endometrial environment (de Mestre, 2013). The most reported age, when the decrease of fertility of the mare starts to be noticeable, is >14 years (Morris and Allen, 2002; Bosh et al., 2009; Nath et al., 2010; Hanlon et al., 2012; Miyakoshi et al., 2012). On the other hand the old mares tended to deliver bigger (heavier and taller) foals than young ones, which may result in better survival of their foals compared to smaller foals of young mares. Moreover inbreeding did not affect the viability of newborn foals through decreasing their weight or height, although it has been reported, that inbreeding had an influence on metric traits in various species, e.g. in sheep (e.g. Ercanbrack and Knight, 1991; Boujenane and Chami, 1997; Mandal et al., 2002), Saharan arrui (*Ammotragus lervia sahariensis*) (Cassinello, 1997) or harbour seal (*Phoca vitulina*) (Coltman et al., 1998). Therefore our results indicate, that inbreeding as well as the higher age of the mare can be one of the many causes of pregnancy failures in horse mares.

AIM 3: MATERNAL CARE AND INVESTMENT

(3.1) Bartošová, J., Komárková, M., **Dubcová, J.**, Bartoš, L., Pluháček, J., (2011). Concurrent lactation and pregnancy: pregnant domestic horse mares do not increase mother-offspring conflict during intensive lactation. PloS one, 6(8), e22068.

In the third manuscript we documented, how the pregnant mares cope with intensified mother-offspring conflict when they have to divide resources between suckled foal and growing foetus. During the first two trimesters of pregnancy, lactating pregnant mares increased their maternal investment into lactation compared to non-pregnant ones without noticeable negative effect on birth weight of the foetus (*i.e*. upcoming newborn foal). Moreover they provided longer suckling bouts which is in contrast to pregnant captive plain zebras, who had a shorter suckling bouts (Pluhacek et al., 2010a). On the other hand pregnant horse, as well as zebra mares (Pluhacek et al., 2010b), did not reject or terminate suckling of their foals more often than non-pregnant ones. Thus our results indicate compensation of early weaning of the foals of pregnant mares which, would come in late pregnancy as it has been reported through equine species (Tyler, 1972; Duncan et al., 1984b; Pluhacek et al., 2007). It can be expected to find similar mechanism also in other ungulates, but the research in this field should be targeted to prove the restriction of maternal investment (lactation) of pregnant mares to their offspring later.

3.2 Komárková, M., Bartošová, J., **Dubcová, J.**, (2011). Effect of mares' dominance rank on suckling behaviour in the loose housed domestic horses. Applied Animal Behaviour Science. 133, 54– 59.

In the fourth manuscript is described how the dominance relationships and agonistic interactions among mares are responsible for differences in suckling behaviour, not explainable by the foal's age. The significant differences in suckling in relation to mare's dominance rank were discovered. Its seems, that high ranking mares invested more intensively into their offspring, they did not terminated their suckling more often. This is possible thanks to the fact, that dominant mare can defend higher level of accessible resources (Boyd, 1991), which was apparent even under domestic conditions (Ellard and Crowell-Davis, 1989; Weeks et al., 2000). Simultaneously high ranking mares 'aggressively' terminated suckling of low ranking ones, as well as the pregnant mares did the same to nursing herdmates. This finding is quite new among horses since the changes in aggression of pregnant mares have not been reported in literature (Estep et al., 1993; Van Dierendonck et al., 2004). The only similar phenomenon was observed in Jeju pony mares (Rho et al., 2004), whose frequency of aggressive actions per hour increased, as the day of parturition approached, probably in relation to provision adequate space for parturition and protection the newborn. Nevertheless, adult herdmates terminated less than three percent (from more than ten thousand) of observed suckling bouts which indicates negligible effect of grouping mares in limited space on suckling behaviour as found recently also in captive plain zebras (*Equus burchelli*, Pluhacek et al., 2010a). Thus it has been confirmed the functionality of social hierarchy the horses usually establish under natural (Tyler, 1972; Berger, 1977; Keiper and Sambraus, 1986) as well as domestic conditions (Van Dierendonck et al., 1995; Weeks et al., 2000), also in limited space, where the aggression is usually abnormally higher (Tyler, 1972; Hogan et al., 1988). It appears, that under optimal nutritional conditions, dominant mares do not tend to reduce fitness of submissive mares through radical interventions into foal's nutrition, *i.e*. interrupting suckling, in agreement on similar study about captive plain zebras (Pluhacek et al., 2006); and contrary to other studies dealing with similar problematic in natural environment (e.g. Tyler, 1972; Rutberg and Greenberg, 1990).

AIM 4: WEANING, STRESS AND GROWTH

④ **Dubcová, J.**, Bartošová, J., Komárková, M., (*in press*). Effects of Prompt vs. Stepwise Relocation to a Novel Environment on Foals' Responses to Weaning in Domestic Horses (Equus Caballus). Journal of Veterinary Behavior: Clinical Applications and Research.

In the fifth manuscript we studied the influence of subsequent changes in foals' life after the weaning, *i.e*. the separation and moving, on salivary cortisol and growth as a signs of acute and long-term stress. Foals, that experienced deferred moving to the new environment showed almost no changes in cortisol levels after separation, but the increase of their cortisol levels appeared after moving to the rearing farm week later. Similarly foals, which went through both changes at once showed the increase in cortisol levels after separation and moving. This increase in salivary cortisol after separation is in agreement with previous horse studies (Erber et al., 2012; Henry et al., 2012). Moreover it has been reported, that moving (usually by road transport) may cause stress and increase the cortisol release in horses (White et al., 1991; Fazio and Ferlazzo, 2003; Schmidt et al., 2010; Tateo et al., 2012). Most of the foals lost some weight during the first post-weaning or post-moving week, but this short-term decrease was significantly more noticeable in foals experienced deferred moving. Nevertheless, this short-term decrease in weight gain of juveniles during the first days after weaning has been reported not only in horses, where it appears up to three weeks after weaning (Griffin et al., 1995; Rogers et al., 2004; Erber et al., 2012), but also in other domestic species, *i.e*. pigs (e.g. Hoetzel et al., 2011) and cattle (e.g. Sweeney et al., 2010). Since we found large individual variability in both, body weight and cortisol levels in observed foals exposed to both weaning procedures and also the variability in growth in seasons, it has been suggested, that other factors, such as social structure of the group or social relationships among foals might play important role in foals' perception and coping with stressful situations including weaning.

Splitting the subsequent changes (separation and moving) associated with artificial weaning induced lower acute stress levels during each particular intervention, but was more harmful from the long-term perspective, than realizing the changes at once. Our results are in contradiction with findings of recent studies, in which staying in the home environment after weaning has been found to be less stressful, than relocation e.g. in piglets (Ekkel et al., 1995; Puppe et al., 1997), beef calves (Lynch et al., 2011), farmed wapiti calves (Church and Hudson, 1999), as well as horses foals (Nicol et al., 2005). Nevertheless these studies do not describe the effects of possible later removal of the 'home-weaned' offspring to unfamiliar environment except of the study of Lynch et al. (2011). So the further research focused on these later effects is needed.

AIM 5: INBREEDING VS. SOCIAL SUCCESS

⑤ **Dubcová, J.**, Bartošová, J., Komárková, M., (*in prep*). Impact of Inbreeding on Social Behaviour and Dominance Rank in an Inbred Population of Domestic Horses (*Equus caballus*).

In the sixth manuscript we studied the influence of inbreeding on social behaviour and dominance position within the herd. We showed that inbreeding level (ID level) of the mare/weanling did not affect its dominance rank calculating either according to Cluttonbrock et al. (1979) (index of fighting success) or according to Pluhacek et al. (2006) (the number of herd members dominating or being subordinated to the individual). The only comparable study in mandrills also showed that neither social rank of the females nor the acquisition of alpha status in males were dependent on inbreeding (Charpentier et al., 2005). Besides, the older weanlings reached higher dominance positions, independent of their sex and the dominance position of their mothers. Thus it has been shown that age is one of the most important factors for acquisition of dominance position in horses (e.g. Keiper and Sambraus, 1986; Feh, 1988; Weeks et al., 2000; Sigurjonsdottir et al., 2003).

We showed that more inbred weanlings initiate more agonistic interactions (AIA) then less inbred ones. This is quite surprising in comparison with suggestions from literature, that more inbred individuals can be in poorer condition (e.g. because of parasitism (Charpentier et al., 2008b)) and thus they cannot invested so much to energetically costly behaviour like aggression (Charpentier et al., 2008a). The males were, compared to females, more often the initiators of the AIA than recipients. The reason can be the fact, that males need to improve their social skills for better chance to obtain and maintain the harem (Tyler, 1972; Rubenstein, 1981; McCort, 1984; Kaseda et al., 1997; Pacheco and Herrera, 1997).

The inbreeding level did not influence most of the tested variables in our study. Still, the higher ID level may be linked to the social behaviour in domestic horses, but it obviously does not cause any fundamental problems in social integration, respecting of the rules of social living and communication among herdmates. Further research is needed for disentangling the deeper level of relationship between inbreeding and behaviour.

4. CONCLUSION

AIM 1: DOMINANCE POSITION AND MATERNAL EFFECTS

CONCLUSION 1.1: The dominance position of the sub-adult horses was influenced by their age.

CONCLUSION 1.2: The dominance position of the foal was moderately repeatable between those foals born to the same mother in two consecutive seasons.

CONCLUSION 1.3: The dominance position of the sub-adult horses was influenced by the length of their residency within the herd.

CONCLUSION 1.4: The maternal factors (*i.e.* mother's age and dominance position, suckling bout duration and frequency or proportion of suckling bout terminated by mother) did not affect reaching the rank by the offspring.

AIM 2: MATING, PREGNANCY AND INBREEDING

CONCLUSION 2.1: The probability of delivery in mares (foaling rate) with extremely high level of inbreeding decreased.

CONCLUSION 2.2: The probability of giving birth changed with age (old mares had lower probability of conception and delivery of a foal after mating).

CONCLUSION 2.3: The old and mid-aged mares produced heavier and taller foals than young ones.

CONCLUSION 2.4: The level of inbreeding did influence neither the birth weight/height in withers nor the probability of conception.

AIM 3: MATERNAL CARE AND INVESTMENT

CONCLUSION 3.1: Pregnant mares, that nursed a foal seemed to compensate earlier weaning of their foals compared to their non-pregnant herdmates by enhancing their maternal care (nursing) in early pregnancy.

CONCLUSION 3.2: There were no consequences of concurrent pregnancy and suckling in terms of lower birth weight for the future foal (foetus) in mares kept in predator-free environment and under optimal nutrition.

CONCLUSION 3.3: Mare's dominance rank did not influence the probability, that she either rejected or terminated a suckling bout.

CONCLUSION 3.4: Mares' dominance rank and agonistic interactions affected suckling bout duration in the herd of domestic horses kept under limited space condition in the barn.

CONCLUSION 3.5: Pregnant and higher ranked mares did more often terminate suckling bouts of other herdmates compared to non-pregnant herdmates.

CONCLUSION 3.6: Adult herdmates had a negligible effect on suckling behaviour of other mares in limited space.

AIM 4: WEANING, STRESS AND GROWTH

CONCLUSION 4.1: Abrupt weaning from mother caused short-term, as well as long-term stress for the foal.

CONCLUSION 4.2: More radical way of moving the weanlings to the new facility was less stressful than stepwise one from the long-term perspective, but it caused higher acute stress.

CONCLUSION 4.3: Foals' coping with weaning depended most likely also on other factors, such as personality or social structure in a given herd.

AIM 5: INBREEDING VS. SOCIAL SUCCESS

CONCLUSION 5.1: The probability of initiation of the agonistic interaction was influenced by the inbreeding level, the age and sex of the individual.

CONCLUSION 5.2: The acquisition of dominance position in the mares/weanlings was not influenced by the inbreeding level of the individual.

CONCLUSION 5.3: The dominance position of the weanling was influenced by its age.

5. PERSPECTIVES

Present thesis provides a complex and comprehensive view on special topics in horse reproduction and offspring development under human management as well as deeper insight into the social behaviour of horses. It contributes to improvement of welfare of horses during suckling and (post-)weaning periods. Finally, it brings novel and important information about breeding and inbreeding in a small endangered population of domestic horses that not only enriched the current scientific knowledge but will serve to breeding management.

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7. Supplement

List of publications:

① Komárková, M., Bartošová, J., Dubcová, J., (2014). Age and group residence but not maternal dominance affect dominance rank in young domestic horses. Journal of Animal Science. 92:5285-5292.

② Dubcová, J., Bartošová, J., (*in prep*). Lower reproductive success in highly inbred domestic horse mares: A message from 70 years of breeding history of an endangered population.

(3.1) Bartošová, J., Komárková, M., Dubcová, J., Bartoš, L., Pluháček, J., (2011). Concurrent lactation and pregnancy: pregnant domestic horse mares do not increase mother-offspring conflict during intensive lactation. PloS one, 6(8), e22068.

(3.2) Komárková, M., Bartošová, J., Dubcová, J., (2011). Effect of mares' dominance rank on suckling behaviour in the loose housed domestic horses. Applied Animal Behaviour Science. 133, 54– 59.

④ Dubcová, J., Bartošová, J., Komárková, M., (*in press*). Effects of Prompt vs. Stepwise Relocation to a Novel Environment on Foals' Responses to Weaning in Domestic Horses (*Equus Caballus*). Journal of Veterinary Behavior: Clinical Applications and Research.

⑤ Dubcová, J., Bartošová, J., Komárková, M., (*in prep*). Impact of Inbreeding on Social Behavior and Dominance Rank in an Inbred Population of Domestic Horses (*Equus caballus*).

1

Komárková, M., Bartošová, J., Dubcová, J. (2014). Age and group residence but not maternal dominance affect dominance rank in young domestic horses. Journal of Animal Science. 92:5285-5292.

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Age and group residence but not maternal dominance affect dominance rank in young domestic horses

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Age and group residence but not maternal dominance affect dominance rank in young domestic horses[1, 2]

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ABSTRACT: We present a study focused on those factors influencing dominance position in young horses, with emphasis on the role of the mother. Horses, as other group-living polygynous mammals, form stable linear dominance hierarchies based on agonistic interactions. Higher dominance positions are believed to be connected, in both sexes, to better condition and higher reproductive success. Many variables play a role in forming the dominant-submissive relationships between horses; however, the maternal effect on the dominance position of the offspring still remains unclear, as do the possible mechanisms of transference ("inheritance"). We hypothesized that the maternal dominance position, plus differences in suckling parameters or maternal style, may be responsible for later outcome of the offspring's dominance position, characterized by 2 variables: index of fighting success (CB); and rate of winning encounters (RW). Our study animals were 8 groups of Kladruby horses, loose-housed lactating mares with foals ($n = 66$ mare-foal pairs); and subsequently 4 groups of the same foals at 3 yr of age. Our results revealed the impact of age on the dominance position of the young horses ($P < 0.001$ for CB, and $P < 0.01$ for RW), and residence in the group ($P < 0.01$, $P < 0.01$, respectively); not the maternal dominance position. Older foals reached higher dominance positions, independent of the dominance position, age, or experience of the mother; therefore, we did not find support for direct inheritance of maternal rank. Nevertheless, the foals born to the same mare in 2 consecutive seasons ($n = 16$ mares) revealed fair repeatability in the dominance position they obtained at 3 yr of age (intraclass correlation coefficient = 0.46). This suggests an important constant effect of the mother on the social success of her progeny; however, we did not find a significant effect of any of the tested variables describing maternal characteristics or maternal care. Dominance position depended significantly on the foal's age at observation, and the residence in the herd formed via sequential introducing of later-weaned groups of foals. The most dominant horses were mainly recruited from the first-weaned group of the season, and thus were also the oldest individuals in the herd. Further research is needed to discover the role of foal personality and mare style, and their links to possible dominance behaviors in a herd.

Key words: age, dominance rank, horse, individuality, mare, residence

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INTRODUCTION

In many group-living polygynous mammals, the individuals profit from higher dominance rank within hierarchies based on agonistic interactions among herd members (Smuts et al., 1987; Weeks et al., 2000; Pluháček et al., 2006). Many variables play a role in forming the dominance hierarchy in young animals: body size (Tyler 1972; Clutton-Brock et al., 1982), age (Pusey and Packer, 1997), residence in the group (Van Dierendonck et al., 1995; Heitor et al., 2006), aggression (Weeks et al., 2000), sex (Araba and Crowell-Davis, 1994) or play behavior (Cameron et al., 2008). Also mothers may affect the dominance rank of

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2

Dubcová, J., Bartošová, J., (*in prep*). Lower reproductive success in highly inbred domestic horse mares: A message from 70 years of breeding history of an endangered population.

Lower reproductive success in highly inbred domestic horse mares: A message from 70 years of breeding history of an endangered population

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Abstract

Inbreeding, *i.e*. mating of related individuals, has been known to bring about a reduction of offspring as well as adults fitness in various species of animals. In the present study we investigated the effect of inbreeding on reproduction-related traits in Kladruby horse, the native Czech breed which passed through several bottlenecks and it is closed for crossbreeding now. The data about reproduction of 1057 mares were used for determination the reproduction-related variables, *i.e*. the pregnancy rate and foaling rates/viable foaling rates (either from mated or pregnant mares). Inbreeding level in studied mares, born from 1900 to 2006, ranged from 0 to 0.27 (mean±SD: 0.035±0.032, median = 0.031, Q3 = 0.047). The mares classified as extreme-inbred ($Fx \geq 0.125$) had significantly decreased foaling rates ($P < 0.05$). The probability of conceiving (pregnancy rate) was not affected with mare's inbreeding level ($P = 0.124$). The age category of the mare had an influence on all of tested reproduction variables ($P < 0.0001$); old mares gave birth less probably than their young or mid-aged herdmates. Birth weight of the foal was not influenced by inbreeding level of the mother ($P = 0.39$) but tended to differ according to her age category ($P = 0.0543$). Mid-aged and old mares tended to deliver heavier foals than young mares. We showed that mare's inbreeding level may unfavourably influence foaling rates in Kladruby horses, and through this it may increase pregnancy losses and decrease their reproduction success. Likewise, we confirmed the importance of mare's age in reproduction of horses.

3.1

Bartošová, J., Komárková, M., Dubcová, J., Bartoš, L., PluháĻek, J., (2011). Concurrent lactation and pregnancy: pregnant domestic horse mares do not increase mother-offspring conflict during intensive lactation. PloS one, 6(8), e22068.

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PLoS one

Concurrent Lactation and Pregnancy: Pregnant Domestic Horse Mares Do Not Increase Mother-Offspring Conflict during Intensive Lactation

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Abstract

Lactation is the most energy demanding part of parental care in mammals, so parent-offspring conflict arises over milk provided by the mother. In some species females commonly become pregnant shortly after parturition of previous young. This further intensifies mother-offspring conflict due to concurrent pregnancy and lactation. In equids it has been well established that pregnant females wean their foals earlier than non-pregnant ones. Intensified mother-offspring conflict was presumed to associate with pregnancy also during the period of intensive lactation, i.e., before the weaning process starts. We investigated the effect of pregnancy on suckling behaviour characteristics as indicators of mother-offspring conflict in domestic horses. Contrary to expectation, here we provide evidence of a decreased mother-offspring conflict related to pregnancy in lactating females during first two trimesters of pregnancy. Pregnant mares provided longer suckling bouts and did not reject or terminate suckling of their foals more often than non-pregnant mares. Our results suggest that pregnant mares cope with parallel investment into a nursed foal and a foetus through enhancing nursing behaviour in early stages of pregnancy before the initially low requirements of the foetus increase. They compensate their suckling foal with the perspective of its early weaning due to ongoing pregnancy.

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Introduction

Among mammals, lactation is the most energy demanding part of parental care [1], so parent-offspring conflict [2] is expected over milk provided by the mother. In particular, parent and offspring should disagree over how long the period of the parental investment should last and over the amount of parental investment that should be provided [2].

In some species, females commonly become pregnant shortly after parturition of previous young, which further intensifies mother-offspring conflict due to concurrent pregnancy and intensive lactation, e.g., in many small rodents and lagomorphs [3–5] or some ungulate species, including equids [6–8]. In horses, lactating mares under natural conditions usually get pregnant again during the first or second oestrus after giving birth (e.g., [6,7,9] post-partum mares experience oestrus, commonly called "foal heat", during the first week after birth [9].

The mares of free living horses [6,10,11] follow the general assumption that the optimum weaning time for pregnant mothers conceiving shortly after giving birth should be earlier than for non-pregnant ones [12]. Earlier weaning in pregnant mares was apparent even in plains zebra mares kept in captivity under optimal nutritional conditions [13]. Females of equid species time weaning according to the expected date of next delivery [7,11,13,14].

While these studies demonstrate well the crucial impact of pregnancy in lactating equid female on mother-offspring conflict over the period of the parental investment (i.e., weaning conflict), little is known about how mother's pregnancy influences conflict between the mother and her offspring over the amount of parental investment she provides during lactation. It was found only recently that in captive plains zebra there are shorter suckling bouts in pregnant mares than non-pregnant ones, suggesting higher mother-offspring conflict when the mother was pregnant [15].

Although suckling behaviour was not found a reliable indicator of milk or energy intake [16], even in foals [17], it can be considered as the behavioural measure associated with parent-offspring conflict over maternal resources [16,17] and as the measure of the level of maternal care provided by the mother in contrast with foal's needs [10,18,19]. Termination of suckling seems to be of great importance. Suckling bouts terminated by the mother are usually shorter compared to those terminated by the foal [15,20]. As such, it probably indicates that the foal was not satiated [17].

In the present study, we tested effect of pregnancy on suckling behaviour variables as indicators of mother-offspring conflict in domestic horses. We hypothesised shorter suckling bouts and higher rates of rejected and/or terminated suckling in pregnant mares compared to non-pregnant ones caused by increased

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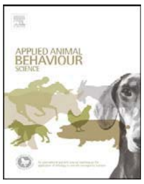

Effect of mares' dominance rank on suckling behaviour in the loose housed domestic horses

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ABSTRACT

Suckling is a main part of maternal investment in equids. The suckling period is crucial for adequate physical as well as psychical development of the foal. The rank of the mother and her aggressiveness could be factors responsible for later reproductive or social success of the foal. We hypothesised that under conditions characterized by balanced diet adjusted to the needs of lactating mares, but limited space, that the dominance relationships and agonistic interactions among mares are responsible for differences in suckling behaviour which cannot be explained by the foal's age. The studied animals were eight groups of loose-housed lactating mares with foals of Kladruby horse. In total, 79 foals (32 males, 47 females) were born to 59 individual mares within two seasons. Not frequency, but suckling bout duration was correlated to the dominance rank of the mare ($P < 0.01$). In addition to lower direct intervention by subordinate herdmates the longer suckling bouts in higher ranked mares reflected higher amount of maternal care the mare provides to her foal. In our study, mares which were more frequently targets of interventions by their dominant herdmates during suckling were also the younger ones ($P < 0.05$). This further supports the role of dominance relationships in alteration of suckling behaviour. Nevertheless, from the practical point of view, the mares' aggressiveness towards other adult herdmates was low and not severe. As such, according to the horse management, it seemed to have only limited practical impact on suckling behaviour in the herd. From this point of view loose housing could be recommended as appropriate housing, even for lactating mares with foals.

1. Introduction

Suckling, the main part of maternal investment in equids, is crucial for the foal development (e.g. Cameron et al., 2003; Cameron and Linklater, 2000). Differences in suckling behaviour could affect later quality of the social and reproductive behaviour of the foal e.g. higher dominance rank and earlier pregnancy in mares or higher probability of own harem formation in stallions (Linklater et al., 1999; Tyler, 1972; Van Dierendonck et al., 1995). High ranking mares are assumed to be in better body condition due to priority of access to food, as well as having a decreased chance of body injury resulting from the receipt of aggression (Weeks et al., 2000). The more dominant the more successful an individual is in chasing others from food or water sources (Duncan, 1992). Due to priority of access to resources the dominant females can invest more energy in offspring, which could lead to higher dominant status of their foal (Boyd, 1991; Weeks et al., 2000). Foals of higher ranking mares can be also more effectively protected from aggression from other herd members (Tyler, 1972). Moreover, dominant mares were found to actively terminate suckling to submissive mares with bites and threats (Lloyd and Rasa, 1989; Pluháček et al., 2010;

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Effects of Prompt vs. Stepwise Relocation to a Novel Environment on Foals’ Responses to Weaning in Domestic Horses (*Equus Caballus*)

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Abstract

Artificial weaning is often highly stressful for both mother and offspring. We investigated the impact of two different time schedules of relocation to a new environment after abrupt weaning on growth rate and saliva cortisol concentrations in a group of loose-housed domestic horses. We predicted higher acute stress (cortisol concentrations), but a lower long-term impact on weight gain indicating lower chronic stress in foals being moved to the new environment immediately after separation from the mothers (‘prompt relocation’, PR) than when relocation was adjourned for a week (‘stepwise relocation’, SWR). Within two seasons, 56 foals weaned at age of 165 to 250 days were regularly weighed up to 140 days after weaning. Growth rate significantly differed between SWR and PR foals. PR weanlings revealed relatively stable increase in their weights while SWR foals experienced a significant drop in growth during the first three weeks after weaning. The weight differences were still apparent five months after weaning (LSMEANs ± SE: 374.40 ± 1.75 kg in PR vs. 362.71 ± 1.66 kg in SWR foals). Cortisol concentrations changed significantly between and within different weaning procedures and were highest in PR foals after weaning and relocation. Compared to pre-weaning values, cortisol levels increased in PR but not in SWR foals, either after weaning or deferred moving. We found large individual variability in foals’ growth as well as cortisol concentrations in both weaning procedures in both weaning types and year effect in stepwise relocated foals. In conclusion, stepwise changes of the physical and social environment within short period after abrupt weaning (deferred removal to the remote facility) resulted in lower acute stress but induced long-term negative effects on foals' growth rate compared to joint weaning and relocation. Our results support rather prompt moving the weanlings to the new facility than the stepwise one on horse breeding farms.

Keywords: weaning, weaning distress, relocation, familiar environment, growth, domestic horses

Introduction

The breaking of the mother-offspring bond (whether natural or forced) often constitutes a highly stressful event for both mother and offspring, especially in the case of the artificial weaning of domestic animals (e.g. Weary, Jasper et al., 2008). Recent pressure to improve the quality of welfare in animal management systems invites further discussion about weaning as a process and a need for scientific investigations of the welfare consequences of alternative weaning methods, better to inform future management practice.

Natural weaning in equids is a gradual process that starts at about 8 months of age and its termination depends mostly on the mare's body condition and her reproductive status; pregnant mares usually wean their foals before one year of age when the next delivery approaches, while mares who failed to conceive in a subsequent season may commonly continue to nurse their yearlings up to two years of age (e.g. Duncan, Harvey et al., 1984; Berger, 1986; Rutberg & Keiper, 1993; Cameron, Linklater et al., 2000; Crowell-Davis & Weeks, 2005; Pluháček, Bartoš et al., 2007). Cessation of milk support, however, does not usually break the mother-offspring bond which frequently persists for several years in many mammalian species (reviewed in Newberry & Swanson, 2008), including horses where the bond between mother and offspring remains strong until the foal leaves the natal group at an age from 1 to 4 years (Tyler, 1972; Monard & Duncan, 1996; Khalil & Kaseda, 1997; Waring, 2003).

By contrast, foals born to domestic horses experience artificial weaning at much younger age than in the wild and this includes nutritional, social, as well as environmental changes, with possible long-lasting consequences for both mother and foal (e.g. Apter & Householder, 1996;

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Impact of Inbreeding on Social Behaviour and Dominance Rank in Domestic Horses (*Equus caballus*)

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Abstract

The relationship between inbreeding, *i.e*. mating of related individuals, and fitness-related variables have been well studied in various species, revealing a detrimental effect of inbreeding in both captive and wild species. However, studies focused on relationship between inbreeding and behaviour, be it parental, sexual, social or other, are rare. In the present study we focused on the influence of inbreeding on social behaviour and dominance of Kladruby horse, Czech native breed with limited population size (around 1500 individuals). We hypothesised that horses with higher level of inbreeding would have lower dominance rank within the herd and that they would initiate and participate in less both, agonistic and non-agonistic interactions. In total 71 mares and their 113 foals (51 males, 62 females) born within three consecutive seasons were observed in the National stud Kladruby nad Labem before and after abrupt weaning. The coefficient of inbreeding (calculated from pedigree from 10 generations according to Wright (1922)) ranged from 0.122 to 0.187. Dominance of the mares/weanlings was characterized by index of fighting success (according to Cluttonbrock et al. (1979)), as well as the number of herd members dominating or being subordinated to the individual (according to Pluhacek et al. (2006)). None of these variables was significantly influenced by inbreeding level. The dominance rank of the weanling depended on its age at observation ($p < 0.01$); the older weanlings reached higher dominance rank, regardless their sex or the dominance rank of the mother. Almost no of the variables describing social behaviour (number of interactions; proportion of agonistic, contact and play interactions; probability of initiation of non-agonistic interaction) was significantly influenced by inbreeding level, except for more inbred weanlings initiated more agonistic interactions then less inbred ones ($p < 0.05$). In addition to this, male ($p < 0.05$) and older ($p < 0.01$) weanlings more often initiated agonistic interaction compared to female or younger herd members. In conclusion, inbreeding level did not significantly influence either dominance rank or the most of the variables describing social behaviour in our study of inbred population of horses.

Introduction

Inbreeding, *i.e.* mating of related individuals, redistribute the frequency of genotypes and causes inbreeding depression so that proportion of homozygotes increases and correspondingly proportion of heterozygotes decreases in the population (Crow, 1948; Lacy, 1997; Keller and Waller, 2002; Charlesworth and Willis, 2009). Inbreeding was observed to lower the fitness-related traits in many species, including humans (e.g. reviewed in: Jimenez et al., 1994; Keller and Waller, 2002; Kristensen and Sorensen, 2005; Charlesworth and Willis, 2009). However, its effect may differ between natural and captive conditions (Ralls et al., 1988; Jimenez et al., 1994; Crnokrak and Roff, 1999). Likewise, it does not affect all traits (fitness vs. non-fitness) to the same degree because the life history traits have greater directional dominance (*i.e.* they are affected by a larger number of single traits and thus a larger number of loci) and hence should show greater inbreeding depression than morphological traits (Crnokrak and Roff, 1995; DeRose and Roff, 1999; Wright et al., 2008). The traits affected by inbreeding may also mutually interact in reducing overall fitness (Kristensen and Sorensen, 2005).

In comparison with widely studied relationship between inbreeding and fitness, relatively little is known about the effects of inbreeding on animal behaviour, either parental, sexual, social or other. Only several studies reported a detrimental effect of inbreeding on behaviour in both invertebrate and vertebrate species; e.g. in crickets (Drayton et al., 2011), snails (Janicke et al., 2014), fish (Tiira et al., 2003; Gallardo and Neira, 2005; Mariette et al., 2006; Ala-Honkola et al., 2009), rodents (Eklund, 1996; Margulis, 1997; Välimäki et al., 2007), primates (Charpentier et al., 2008) and humans (Fareed and Afzal, 2014a). Higher dominance rank within the social hierarchy is usually associated with better condition and higher reproductive success in many group-living mammals (Cassinello and Alados, 1996; Pusey et al., 1997; Weeks et al., 2000; Pluhacek et al., 2006) and attributed to morphological characteristics, like weight (Houpt et al., 1978; Ellard and Crowell-Davis, 1989) or height (Ellard and Crowell-Davis, 1989; Rutberg and Greenberg, 1990). Little attention was paid to the genetic background of the individuals. Charpentier et al. (2008) showed that female