Published November 20, 2014

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

**M. Komárková[3], J. Bartošová, and J. Dubcová**

Department of Ethology, Institute of Animal Science, Přátelství 815, Prague-Uhříněves, Czech Republic 104 00

**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



J. Anim. Sci. 2014.92:5285–5292
doi:10.2527/jas2014-7674

## 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

[1]This study was supported by the Ministry of Agriculture of the Czech Republic (Project MZe0002701404), and by EU VII Framework program (FP7-KBBE-2010–4, "AWIN").

[2]Authors would like to thank the former and current directors of the National stud, Kladruby nad Labem for enabling the study, as well as the staff, viz. E. Kozlová and the team from Selmice for their enthusiasm and excellent field assistance. They are also grateful to J. Komárková and M. Komárková for their help with data collection. Authors highly appreciated the comments of F. Ceacero, J. Pluháček and R. Šárová, as well as those of the anonymous referees. Thanks to P. Lemkin for improving the English.

[3]Corresponding author: eto89@seznam.cz

Received January 29, 2014.
Accepted September 16, 2014.

their offspring (Green and Rothstein, 1993; Van Dierendonck et al., 1995). On the one hand, higher dominance rank has been suggested in foals subjected to higher maternal care and protectiveness (Hewison and Gaillard, 1999; Heitor and Vicente, 2008). Mothers giving birth early in the season (Wells and von Goldschmidt-Rothschild, 1979; Green and Rothstein, 1993) may produce larger offspring with higher rank compared to herdmates born later in the year. On the other hand, the possible transference ("inheritance") of the dominance rank from the mother to the offspring remains unclear (Green and Rothstein, 1993; Van Dierendonck et al., 1995). Horses, with their complex social system, based on agonistic interactions and a long period of maternal care, are a valuable model for the study of maternal effects on offspring rank.

Based on our previous results that the dominant mares nursed their foals longer and terminated fewer suckling bouts (Komárková et al., 2011), we investigated how the maternal characteristics and care underlie the foal's social dominance. We hypothesized that the offspring of dominant mares will reach a higher rank than the progeny of subordinate mares, due to more intense maternal care. We also examined the repeatability of dominance status and maternal care in foals born to the same mare in consecutive seasons, indicating maternal influence.

## MATERIALS AND METHODS

This study received approval for animal use and care from The Institutional Animal Care and Use Committee of the Institute of Animal Science, and was conducted in accordance with the Czech Central Committee for Protection of Animals law number 13803/2003–1020.

### *Mares with Foals*

The animals studied were 8 groups of Kladruby horses, lactating mares with foals, loose-housed at the National Stud, Kladruby nad Labem, Czech Republic (50°3'8.253"N, 15°26'19.148"E). The groups further contained up to 5 mares with foals of Czech warm-blooded horses, but they did not enter into the analyses because of possible breed-dependent differences; however, the dominance ranks of the mares were calculated with respect to all herdmates involved in the social interactions. In total, 79 foals (32 males, 47 females) were born to 59 individual mares during 2 seasons (containing 41 and 38 foals, respectively). Four mare-foal pairs, where the mares were forced to adopt an orphan foal by the farm managers, were excluded from the data set. Further reductions of the number of animals were due to deaths, removal from the herd by stud management, or different styles of weaning (1 female was weaned alone). Altogether, 66 foals (29 males, 37 females) born to 50 individual mares (16 mares gave birth in both observational seasons) were analyzed. The mares were aged from 4 to 25 yr, and were classified into 3 categories, according to Carnevale and Ginther (1992): 4 to 7 yr old mares were classified as young, 8 to 14 yr old as middle-aged, and 15+ yr as old. Ten mares were primiparous. Multiparous mares had previously given birth to from 1 to 12 foals. The groups were formed and managed as follows. Each season, pregnant mares were divided into 4 groups of 8 to 14 mares each, according to their expected date of delivery, and housed in barns of 10 × 35 m. The mares gave birth within the group within the barn; a veterinarian assisted only if health complications arose. Animals from all groups were joined, and pastured together daily from 0900 to 1500 h. The mares were tied and fed individually with oats, minerals, and vitamins each morning. Hay was served daily on an ad libitum basis. The foals had free access to the food served to their mothers.

The groups of mares with foals were observed from the time the group was formed and contained at least 5 mother-foal pairs (on average, 14 d after first foal delivery) until abrupt weaning. The length of time a particular foal was observed differed according to its date of birth, group, and time of weaning. Therefore, we limited the 'nursing period,' which was further analyzed in this study, to that data collected between 25 and 127 d of the foals' age. The beginning of this period overlaps with the onset of increased social activities in the foals (Crowell-Davis et al., 1987; Boyd, 1988; McDonnell and Poulin, 2002). The end of this period corresponds to the end of peak lactation in horse mares (Davies Morel, 2008). Newborn foals were weighed within 1 d after parturition by the stud staff. The observation protocol during lactation replicated that of other studies of maternal behaviors in equids (Cameron et al., 1999; Pluháček et al., 2010; for details see Komárková et al., 2011). Each group was observed in the barn every second week in two 3-h sessions ("observation session") from 0330 to 0630 h in the morning and from 1500 to 1800 h in the evening. The ad libitum sampling method (Altmann, 1974) was applied to record suckling occurring in the herd. We recorded suckling bouts and the terminator of each suckling bout was assessed: mother, foal, other herdmates, or an unexpected event in the environment of the horse ('other'). For each foal, we calculated the mean suckling bout durations, mean frequency of suckling bouts recorded per 6 h observation session, and the proportion of suckling bouts terminated by the mother over the entire observation period.

### *Weaning*

The foals were abruptly weaned between 4 to 7 mo of age, depending on stud management. They were weaned in groups with respect to their ages, on 4 successive dates ('weaning dates'; in September, October, November of

each year and January of the second year only). A group of weanlings was moved to another facility belonging to the National Stud, which served for rearing youngsters ('rearing stable', 50°3'8.253"N, 15°26'19.148"E) that were loose-housed in a barn. Newer groups of weanlings, born in the same season, were introduced into the same barn and formed 1 group. The foals were sex-separated 1 mo after the last weanling group arrived into 2 herds (1 male group and 1 female group), and were kept like this up to the age of 3 yr. Apart from the Kladruby horses, Czech warm-blooded horse foals were kept within the groups, and they entered the analyses only for the purpose of calculating social interactions. Foals experienced a similar daily regime, as before, with their mothers. Horses were loose-housed, and from 0900 to 1500 h they were in the pasture. Weighing was done regularly twice a year.

### *Assessing Dominance Hierarchy*

The dominance hierarchy assessment was based on ad libitum sampling (Altmann, 1974) of agonistic interactions among the group members. Interactions among the mares were recorded in each mare-foal group during observations of the suckling behaviors. In addition to this, the hay was served to provoke higher number of agonistic interactions among mares once in each observation session. Each herd of offspring was observed for 6 h for 5 d (i.e., 30 h in total) on the pasture. The food competition was initiated 3 times during each observational session (one 10-L bucket of oats was divided to 3 piles placed 3 m from one another). Horse-horse encounters recorded were classified as dominant if they involved: head, bite or kick non-contact threats; biting and/or offensive kicking. They were classified as submissive if they involved defensive kicking and displacement (as described in Araba and Crowell-Davis, 1994; Pluháček et al., 2006). The winner and loser of every encounter was determined. The dominance position of each individual was calculated as the mare's or young horse's index of fighting success according to Clutton-Brock et al. (1979). The Clutton-Brock index (CB) was as follows: $CB = (B + \Sigma b + 1)/(L + \Sigma l + 1)$, where B is the number of animals which the focal animal had beaten; $\Sigma b$ = the total number which they beaten, excluding the subject; L = the number of animals to which the focal animal had lost; and $\Sigma l$ = the total number to which the animals that beat the focal one had lost, excluding the subject. The addition of 1 to each side of the ratio reduces the chance of an anomalous result occurring in cases where individuals were either never observed to beat other animals or never observed to be beaten (Clutton-Brock et al., 1979). As the number of horses per group varied, the resulting dominance index was divided by the number of mares (or offspring) in the herd. In addition to the CB, we calculated the rate of winning encounters (RW = number of encounters the horse won/number of all encounters the horse was involved in). The RW describes the individual's overall fighting success in encounters, while the CB rates the individual's dominant and submissive relationships within its herdmates. As expected, CB and RW highly correlated to one another in the observed groups, in both the mothers as well as the young (Spearman correlation coefficients higher than +0.72). The individuals with a higher proportion of winning interactions also reached higher dominance positions.

### *Statistical Analyses*

The statistical analyses were performed using SAS 9.3 (SAS Inst. Inc., Cary, NC). Neither the CB nor RW variables were normally distributed (Kolmogorov-Smirnov test). Therefore, nonparametric statistical tests were employed in the exploratory analyses, and a lognormal distribution was specified when fitting the linear models. Relationships between the variables investigated were explored using Spearman correlation coefficients for continuous variables (procedure PROC CORR, SAS), and the Kruskal–Wallis test for investigation of continuous differences, according to class of the variable (PROC NPAR1WAY, SAS).

The repeatability of CB and RW in mothers observed in both seasons and their foals was estimated via the intraclass correlation coefficient (ICC). The ICC was derived from covariance and residual variance parameters (see the formula below); estimated via a general fitting linear mixed model (PROC MIXED, SAS) with log-transformed CB (or RW) as the dependent variable, and season as a fixed effect. The identity of the mother specified repeated measures in different seasons (REPEATED statement with compound symmetry covariance structure). The ICC was calculated as: covariance parameter/(covariance parameter + residual variance parameter). According to Fleiss (1986), an ICC < 0.4 indicates poor repeatability, 0.4 to 0.75 fair to good, and > 0.75 good to excellent repeatability.

The impact of the factors tested on the CB and RW was assessed via the fitting of generalized linear mixed models (GLMM, PROC GLIMMIX, SAS). The CB (or RW) entered the model as a dependent variable, and the lognormal distribution with identity link function was specified. The fixed effects were the age of the foal at observation plus the following variables, which represented the maternal influence: mother's age category (young, middle age, or old), mother's dominance success (either CB or RW, corresponding to the dependent variable), mean suckling bout durations, as well as the mean frequency and proportion of suckling bouts terminated by the mother. Those measures obtained on foals born to the

**Table 1.** Number of young horses and their agonistic interactions in 2 seasons

| | Male season 1 | Female season 1 | Male season 2 | Female season 2 |
|---|---|---|---|---|
| Kladruby horse | 16 | 23 | 17 | 22 |
| Other breed | 0 | 0 | 8 | 5 |
| Agonistic interactions | 611 | 1,242 | 1,601 | 2,363 |

**Table 2.** Mean values for indices of dominance position for both mares and foals; CB: index of fighting success calculated according to Clutton-Brock et al. (1979), and RW: rate of winning encounters

| | Maternal CB | Maternal RW | Foals CB | Foals RW |
|---|---|---|---|---|
| Mean ± SD | 0.38 ± 0.84 | 0.47 ± 0.30 | 0.57 ± 1.78 | 0.38 ± 0.26 |
| Minimum | 0.0015 | 0.02 | 0.00035 | 0 |
| Maximum | 5.08 | 1.00 | 8.59 | 0.99 |

same mother but in different seasons were specified in the RANDOM statement. The significance of each fixed effect in the GLMM was assessed using the *F*-test.

Relationships between birth weight, weight at observation, and the suckling variables of the foals ($n$ = 32) born to the same mothers ($n$ = 16) were explored using the partial Pearson or Spearman correlation coefficient (PROC CORR, SAS). The age at observation was treated as a partial variable, to control the relationships between the tested variables for the strong effect of correlation between the ages of the foals born in different seasons ($r = 0.79$, $P < 0.001$).

## RESULTS

In total, 10,607 suckling bouts within 516 h of observation were recorded, with a mean suckling bout duration of 73.8 ± 28.9 s (mean ± SEM), and a frequency of 13.0 ± 5.01 suckling bouts per 6 h observation session. Mothers terminated 15% of the suckling bouts, 80% were terminated by the foal, and 3% by a herdmate (see details in Komárková et al., 2011).

We recorded 2,091 agonistic interactions among mares (1,012 and 1,079 interactions in a specific season), ranging from 134 to 356 interactions per group. The numbers of agonistic interactions recorded in the young are shown in Table 1. The values of CB and RW for mothers and foals are described in Table 2.

In young horses, the mean values of neither CB nor RW differed according to sex or season (CB: $\chi^2_3 = 0.16$, $P = 0.98$, RW: $\chi^2_3 = 4.00$, $P = 0.26$, Kruskal–Wallis test). Repeatedly observed mothers mostly kept their CB and RW between seasons ($r$ = 0.82 and 0.83, respectively, intraclass correlation coefficient; Fig. 1). The repeatability of CB and RW in foals born to the same mares was lower but still fair ($r$ = 0.46 and 0.49, respectively, Fig. 1); therefore, the identity of the mother entered further analyses as a random factor.

Both the CB and RW highly increased with the age of the individual at time of observation (CB: $F1,15 = 20.14$, $P < 0.001$, RW: $F1,15 = 13.37$, $P < 0.01$, GLMM); and significantly decreased within weaning dates (CB: $F3,14 = 8.22$, $P < 0.01$, RW: $F3,14 = 6.23$, $P < 0.01$). The most dominant individuals came from the first weaned groups within the season (Fig. 2), with the exception of 1 male group to which the top-ranked stallion had arrived with the second weaned foals (Fig. 2, top right). This stallion showed the highest agonistic activity within the young; he won all of the 1,574 agonistic interactions he initiated, which comprised 67% of all interactions observed in the herd of 25 individuals. The age of the foal at observation and the weaning date were highly correlated ($rs = -0.96$, $P < 0.0001$, $n = 66$) and not mutually independent, because younger foals were weaned later in the season. Age at observation was selected to represent these 2 factors in further analyses.

None of the tested factors characterizing the impact of the mother on foal dominance success at the age of 3 yr (i.e., age and dominance position of the mother, suckling bout duration and frequency, or proportion of suckling bout terminated by the mother) significantly influenced either the CB or RW.

In addition to the repeatability of the offspring CB (RW), described above, we analyzed 16 pairs of full- or half-siblings born to the same mother in 2 consecutive seasons. It did not reveal any significant correlation between their birth weights, weight at observation, or suckling variables. They only shared a similar age at observation ($r = 0.79$, $P < 0.001$).

## DISCUSSION

Our results revealed the primary importance of age of the foal, not maternal dominance position, in the rank acquaintance of the offspring. The Clutton-Brock index (CB) and rate of winning encounters (RW) depended significantly on the age of the foal at observation, as well as residence in the herd formed via sequentially introducing later weaned groups of foals. The most dominant horses were mainly recruited from the first weaned group in a season, and they were also primarily the oldest individuals in the herd. This difference was evident even later than 2 yr after weaning. We also demonstrated a fair repeatability of the dominance position in foals born to the same mother within 2 consecutive years.

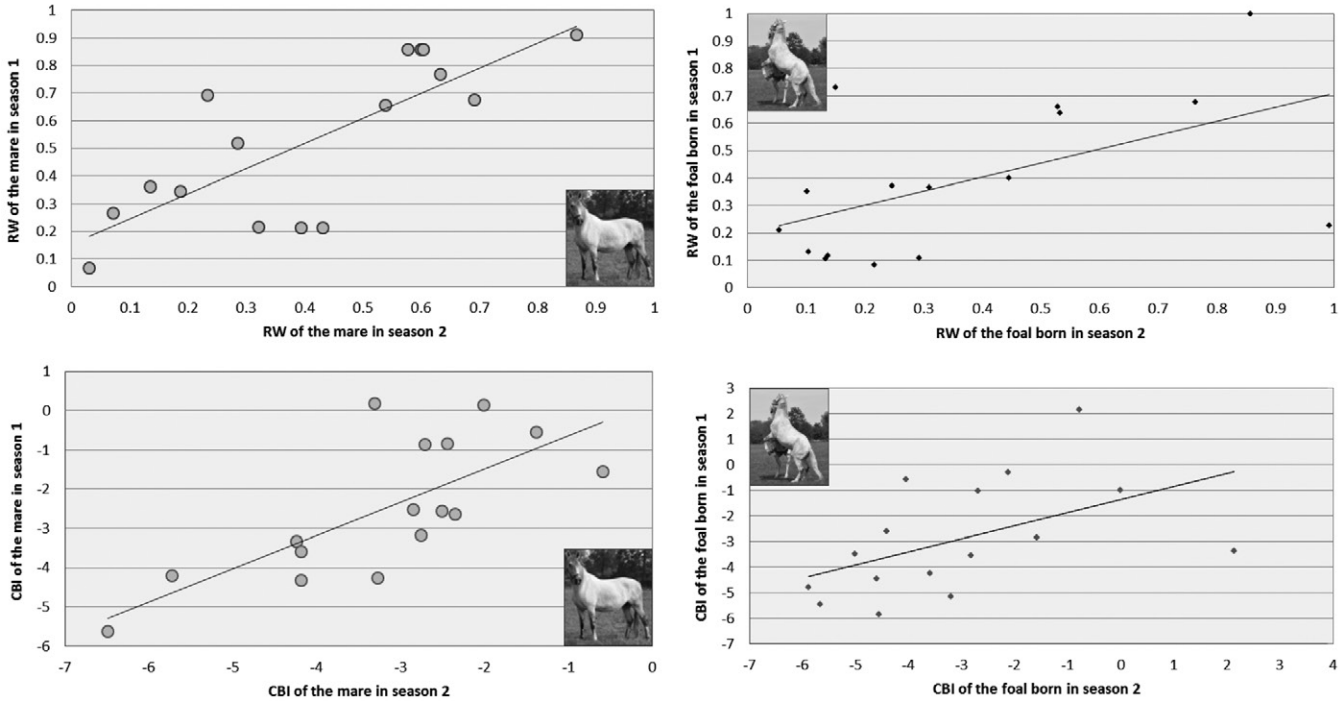


**Figure 1.** Correlation of the dominance rank, represented by the rate of winning encounters (RW, top) and Clutton-Brock index (transformed by natural logarithm, CBI, bottom) in the mares giving birth in 2 consecutive seasons (left, $n = 16$) and their foals at 3 yr of age (right).

### *Age as a Social Advantage*

We showed that foal age is the most important factor influencing their dominance within the herd. The oldest (i.e., first born) foals dominated their younger (later born) herdmates in sub-adulthood. The studies on the effects of the age in hierarchy acquaintance have provided inconsistent results in horse studies. It remains unclear whether older horses always dominate the younger or, most likely, more factors play a role together (Tyler, 1972; Clutton-Brock et al., 1976; Berger, 1977; Houpt et al., 1978; Wells and von Goldschmidt-Rothschild, 1979; Haag et al., 1980; Rubenstein, 1981; Keiper and Sambraus, 1986; Ellard and Crowell-Davis, 1989; Araba and Crowell-Davis, 1994; Weeks et al., 2000; Heitor and Vicente, 2008). The mothers may influence the age and rank of their offspring within the foals born in the same year through timing the delivery; they produce larger offspring with greater fecundity and a higher rank compared to their herdmates born later in the year when giving birth earlier in the season (Wells and von Goldschmidt-Rothschild, 1979; Green and Rothstein, 1993).

As with other highly social species, horses need social experiences to develop appropriate social skills (Waran et al., 2008). Therefore, foals born earlier in the season may profit from the additional time to learn and train their social skills. A lack of juvenile social experience may affect adult social behaviors, especially those related to aggression, as has previously been reported in other social species (cows: Veissier et al., 1994; Bøe and Færevik, 2003). Most changes in the feral horse dominance hierarchies occurred with younger animals (Wells and von Goldschmidt-Rothschild, 1979). When a new horse entered the group the aggression levels increased, but the hierarchy usually stabilized again within 1 wk (Tyler, 1972). So, it seems that for the dispersing of progeny of both sexes, immediate fighting success, leading to a higher ranking in the new harem group, is highly

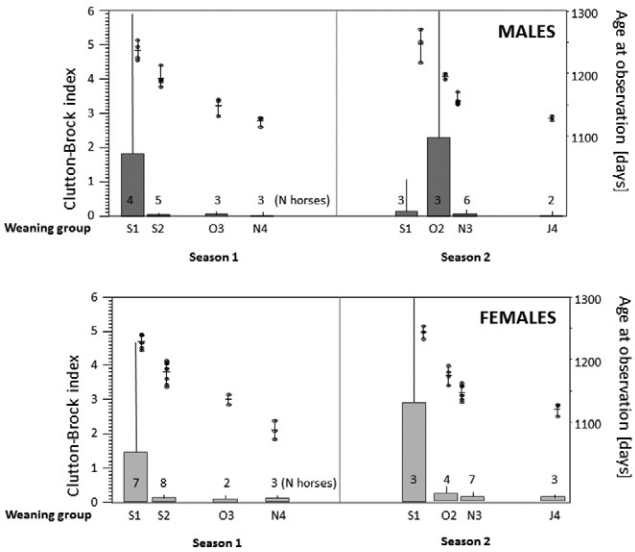


**Figure 2.** Clutton-Brock index (raw data) of the young horses according to date of weaning (left y-axis, grey bars: mean ± SE) and age at observation (right y-axis, black points on solid vertical lines indicating age of individuals and mean age) in males (top) and females (bottom). The number of horses (N horses) weaned in 2 consecutive seasons (Season 1, left; Season 2, right) in the 4 weaning groups (S: September, first and second group; O: October; N: November; J: January) are indicated inside the graphs.

advantageous for obtaining better conditions for obtaining food and/or partners. In other seasonally-breeding ungulates, early birth increased both the viability and social status (Guinness et al., 1978; Dublin, 1983; Festa-Bianchet, 1988; Green and Rothstein, 1993). The advantage of early birth, compared to the other herdmates, persisted in our study up to age 3. Nevertheless, in our study, the timing of births partly reflected breeding management; therefore further research should be aimed at investigating the possible tendencies of mares to time their deliveries earlier in the season.

### *Residence in the Herd*

We found that the foals weaned in the first cluster within a season reached a higher dominance rank than those which joined the herd from any later weaned cluster of foals (but note the exception described previously in the text). The dominance position of a horse seems to be correlated to the length of residency within the herd (e.g., McDonnell and Haviland, 1995; Heitor et al., 2006). In free-ranging as well as captive equids, aggression is most often directed against the newest animal in the group (Wells and von Goldschmidt-Rothschild, 1979; Rutberg, 1990; Rutberg and Greenberg, 1990, Arnold and Grassia, 1982). Dispersed young mares had higher injury/blemish grades compared to resident mares (Grogan and McDonnell, 2005). Exposing resident horses to newcomers has recently been studied in adults (however only in individuals; Hartmann et al., 2011), but information on foals is still lacking.

Due to routine stud practice, the foals weaned in the first cluster were also the oldest ones within a season. Thus, the effects of age and residence could not be separated in our study. Nevertheless, based on the literature cited above, they most likely profited from both their higher age and longer residence time.

### *Maternal Rank Inheritance*

There are 2 suggested mechanisms of maternal rank "inheritance." Females aiding their young in agonistic encounters with other conspecifics may increase the probability their young won an encounter (Tyler, 1972). Alternatively, the mother may preferentially direct aggressive behavior towards the offspring of lower-ranking herdmates (Horrocks and Hunte, 1983; Weeks et al., 2000). Associative learning of the animals involved in these interactions may result in later differences in their position within the hierarchy (Houpt et al., 1978). However, we haven't found evidence of direct maternal rank inheritance in our study. As in the study of Heitor and Vicente (2008), the dominance position of subadult offspring did not correlate to that of its mother, as had been reported in pre-weaned and post-weaned foals (Tyler, 1972; Wells and von Goldschmidt-Rothschild, 1979; Weeks et al., 2000), as well as adult horses (Feh, 1990; Van Dierendonck et al., 1995; Monard and Duncan, 1996

Before artificial weaning, the foals formed unstable dominance hierarchies, and the encounters displayed fighting play rather than real dominance (Tyler, 1972; Wells and von Goldschmidt-Rothschild, 1979; Weeks et al., 2000; Heitor and Vicente, 2008). However, since the horses become sexually mature at 1 to 3 yr (Keiper and Sambraus, 1986; Monard and Duncan, 1996) they often experience intense fights to attain their dominant position within a new herd after leaving their natal band (Waring, 1983). Studies suggesting existing rank inheritance from long-term observations of adult horses either in feral (Camargue stallions: Feh, 1990; mares: Monard and Duncan, 1996) or captive populations (Icelandic horse mares: Van Dierendonck et al., 1995) suffered mostly from low sample size (up to 11 horses). However, unlike studies on horses under domestic conditions (including ours); these were not additionally encumbered with artificial weaning. Artificial weaning is one of the most stressful periods of a foal's life (e.g., Apter and Householder, 1996; Nicol et al., 2005; Mills and McDonnell, 2005), which may disrupt the natural associative learning process in young horses (Nicol, 2002); it also likely influences the acquisition of the dominance position within the social hierarchy.

### *Repeatability of Dominance Rank in Foals Born to the Same Mothers*

Our study revealed moderate repeatability in the dominance rank of foals born to the same mother in 2 consecutive seasons. We did not find any other correlation in the maternal care variables including suckling behavior, birth weights, weights in sub-adulthood, or of the foal characteristics; except for the age at observation (birth date). The earlier the foal was born in the first season, the earlier its mother delivered its sibling the next year. Wells and von Goldschmidt-Rothschild (1979) observed that dominant mares under natural environment gave birth earlier in the season. Under domestic condition, however, the timing of delivery in the mares results mostly from the breeding management (see comments above). Nevertheless, timing of delivery was not the source of significant repeatability of the young horse's dominance position in our study. Thus, the other maternal effects, such as the maternal style, can cause similar dominance positions, which the progeny of individual mares obtained.

Individual females have been found to demonstrate characteristic maternal styles in many species (e.g., Fairbanks, 1996), including horses (Crowell-Davis, 1986), which tend to be constant over time with the same infant,

as well as consistent for individual mothers across other infants (Fairbanks and McGuire, 1988; Berman, 1990).

Various maternal behaviors have been studied (e.g., in primates showing, for example) that a greater independence from the mother, exploration, and involvement in social interactions were found in those offspring which experienced high levels of maternal rejection, compared to more protected "mamma's boys/girls" (Hinde, 1974; Suomi, 1987; Simpson and Datta, 1991). Further research should be aimed at investigating the maternal style and its repeatability in horses where the data, either supportive (Crowell-Davis, 1986; Cameron and Linklater, 2000; Heitor and Vicente, 2008), or not, is rare.

### *Conclusions*

Our results showed the importance of the age of the foal, residence, and some maternal effects on the dominance position of the offspring; however, not the maternal rank. The older foals reached a higher dominance position, which was moderately repeatable between those foals born to the same mother in 2 consecutive seasons. We also found a positive effect of a longer residence of the young horse within the herd.

## LITERATURE CITED


Altmann, J. 1974. Observational study of behavior: Sampling methods. Behaviour 49:227–267.

Apter, R. C., and D. D. Householder. 1996. Weaning and weaning management of foals: A review and some recommendations. J. Equine Vet. Sci. 16:428–435.

Araba, B. D., and S. L. Crowell-Davis. 1994. Dominance relationship and aggression of foals (*Equus caballus*). Appl. Anim. Behav. Sci. 41:1–25.

Arnold, G. W., and A. Grassia. 1982. Ethogram of agonistic behaviour for thoroughbred horses. Appl. Anim. Ethol. 8:5–25.

Berman, C. M. 1990. Consistency in maternal behavior within families of free-ranging rhesus monkeys: An extension of the concept of maternal style. Am. J. Primatol. 22:159–169.

Berger, J. 1977. Organizational systems and dominance in feral horses in the Grand Canyon. Behav. Ecol. Sociobiol. 2:131–146.

Bøe, K. E., and G. Færevik. 2003. Grouping and social preferences in calves, heifers and cows. Appl. Anim. Behav. Sci. 80:175–190.

Boyd, L. E. 1988. Ontogeny of behaviour in Przewalski horses. Appl. Anim. Behav. Sci. 21:41–69.

Cameron, E. Z., K. J. Stafford, W. L. Linklater, and C. J. Veltman. 1999. Suckling behaviour does not measure milk intake in horses, *Equus caballus*. Anim. Behav. 57:673–678.

Cameron, E. Z., and W. L. Linklater. 2000. Individual mares bias investment in sons and daughters in relation to their condition. Anim. Behav. 60:359–367.

Cameron, E. Z., W. L. Linklater, K. J. Stafford, and E. O. Minot. 2008. Maternal investment results in better foal condition through increased play behaviour in horses. Anim. Behav. 76:1511–1518.

Carnevale, E. M., and O. J. Ginther. 1992. Relationships of age to uterine function and reproductive efficiency in mares. Theriogenology 37:1101–1115.

Clutton-Brock, T. H., P. J. Greenwood, and R. P. Powell. 1976. Ranks and relationships in Highland ponies and cows. Z. Tierpsychol. 41:202–216.

Clutton-Brock, T. H., S. D. Albon, R. M. Gibson, and F. E. Guinness. 1979. The logical stag: Adaptive aspects of fighting in red deer (*Cervus elaphus L.*). Anim. Behav. 27:211–225.

Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1982. Competition between female relatives in a matrilineal mammal. Nature 300:178–180.

Crowell-Davis, S. L. 1986. Spatial relations between mares and foals of the Welsh pony, *Equus caballus*. Anim. Behav. 34:1007–1015.

Crowell-Davis, S. L., K. A. Houpt, and L. Kane. 1987. Play development in Welsh pony (*Equus caballus*) foals. Appl. Anim. Behav. Sci. 18:119–131.

Davies Morel, M. C. G. 2008. Equine reproductive physiology, breeding and stud management. 3rd ed. CABI Publishing, Wallingford, UK.

Dublin, H. T. 1983. Cooperation and reproductive competition among female African elephants. In: S.K. Wasser, editor, Social behavior of female vertebrates. Academic Press, New York. p. 291–313.

Ellard, M. E., and S. L. Crowell-Davis. 1989. Evaluations of rank-order, social spacing and aggression in domestic horses (*Equus caballus*). Appl. Anim. Behav. Sci. 24:55–75.

Fairbanks, L. A. 1996. Individual differences in maternal style: Causes and consequences for mothers and offspring. Adv. Stud. Behav. 25:579–611.

Fairbanks, L. A., and M. T. McGuire. 1988. Long-term effects of early mothering behavior on responsiveness to the environment in vervet monkeys. Dev. Psychobiol. 21:711–724.

Feh, C. 1990. Long-term paternity data in relation to different aspects of rank for Camargue stallions, *Equus caballus*. Anim. Behav. 40:995–996.

Festa-Bianchet, M. 1988. Birthdate and survival in bighorn lambs (*Ovis canadensis*). J. Zool. (Lond.) 214:653–661.

Fleiss, J. L. 1986. The design and analysis of clinical experiments. Wiley, New York.

Green, W. C., and A. Rothstein. 1993. Persistent influences of birth date on dominance, growth and reproductive success in bison. J. Zool. (Lond.) 230:177–186.

Grogan, E. H., and S. M. McDonnell. 2005. Injuries and blemishes in a semi-feral herd of ponies. J. Equine Vet. Sci. 25:26–30.

Guinness, F. E., T. H. Clutton-Brock, and S. D. Albon. 1978. Factors affecting calf mortality in red deer (*Cervus elaphus*). J. Anim. Ecol. 47:817–832.

Haag, E. L., R. Rudman, and K. A. Houpt. 1980. Avoidance maze learning and social dominance in ponies. J. Anim. Sci. 50:329–335.

Hartmann, E., L. J. Keeling, and M. Rundgren. 2011. Comparison of 3 methods for mixing unfamiliar horses (*Equus caballus*). J. Vet. Behav. 6:39–49.

Heitor, F., M. D. M. Oom, and L. Vicente. 2006. Social relationships in a herd of Sorraia horses: Part I. Correlates of social dominance and contexts of aggression. Behav. Processes 73:170–177.

Heitor, F., and L. Vicente. 2008. Maternal care and foal social relationships in a herd of Sorraia horses: Influence of maternal rank and experience. Appl. Anim. Behav. Sci. 113:189–205.

Hewison, A. J., and J. M. Gaillard. 1999. Succesful sons or advantaged daughters? The Trivers-Willard model and sex-biased maternal investement in ungulates. Trends Ecol. Evol. 14:229–234.

Hinde, R. A. 1974. Interactions, relationships, and social structure in non-human primates. *In* Symposium of the 5th Congress of the International Primate Society, Nagoya, Japan: p. 13–24.

Horrocks, J., and W. Hunte. 1983. Maternal rank and offspring rank in vervet monkeys: An appraisal of the mechanisms of rank acquisition. Anim. Behav. 31:772–782.

Houpt, K. A., K. Law, and V. Martinisi. 1978. Dominance hierarchies in domestic horses. Appl. Anim. Ethol. 4:273–283.

Keiper, R., and H. H. Sambraus. 1986. The stability of equine dominance hierarchies and the effects of kinship, proximity and foaling status on hierarchy rank. Appl. Anim. Behav. Sci. 16:121–130.

Komárková, M., J. Bartošová, and J. Dubcová. 2011. Effect of mares' dominance rank on suckling behaviour in the loose housed domestic horses. Appl. Anim. Behav. Sci. 133:54–59.

McDonnell, S. M., and J. C. S. Haviland. 1995. Agonistic ethogram of the equid bachelor band. Appl. Anim. Behav. Sci. 43:147–188.

McDonnell, S. M., and A. Poulin. 2002. Equid play ethogram. Appl. Anim. Behav. Sci. 78:263–290.

Mills, D. S., and S. M. McDonnell, editors. 2005. The domestic horse: The origins, development and management of its behaviour. Cambridge Univ. Press, The Edinburgh Building, Cambridge, UK.

Monard, A. M., and P. Duncan. 1996. Consequences of natal dispersal in female horses. Anim. Behav. 52:565–579.

Nicol, C. J. 2002. Equine learning: Progress and suggestions for future research. Appl. Anim. Behav. Sci. 78:193–208.

Nicol, C. J., A. J. Badnell-Waters, R. Bice, A. Kelland, A. D. Wilson, and P. A. Harris. 2005. The effects of diet and weaning method on the behaviour of young horses. Appl. Anim. Behav. Sci. 95:205–221.

Pluháček, J., L. Bartoš, and L. Čulík. 2006. High ranking mares of captive plains zebra *Equus burchellii* have greater reproductive success than low ranking mares. Appl. Anim. Behav. Sci. 99:315–329.

Pluháček, J., L. Bartoš, and J. Bartošová. 2010. Mother–offspring conflict in captive plains zebra (*Equus burchellii*): Suckling bout duration. Appl. Anim. Behav. Sci. 122:127–132.

Pusey, A. E., and C. Packer. 1997. The ecology of relationships. In: J.R. Krebs and N.B. Davies, editors, Behavioural Ecology. An Evolutionary Approach. 4th ed. p. 254–283.

Rubenstein, D. I. 1981. Behavioural ecology of island feral horses. Equine Vet. J. 13:27–34.

Rutberg, A. T. 1990. Inter-group transfer in Assateague pony mares. Anim. Behav. 40:945–952.

Rutberg, A. T., and S. A. Greenberg. 1990. Dominance, aggression frequencies and modes of aggressive competition in feral pony mares. Anim. Behav. 40:322–331.

Simpson, M. J. A., and S. B. Datta. 1991. Predicting infant enterprise from early relationships in rhesus macaques. Behaviour 116(1-2):42–63.

Smuts, B. B., D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker. 1987. Primate societies. University of Chicago Press, Chicago, IL.

Suomi, S. J. 1987. Genetic and maternal contributions to individual differences in rhesus monkey biobehavioral development. In: N. A. Krasnegor, E. M. Blass, and M. A. Hofer, editors, Perinatal development: A psychobiological perspective, Behavioral Biology. Academic Press, San Diego CA. p. 397–419.

Tyler, S. J. 1972. The behaviour and social organization of the New Forest ponies. Anim. Behav. Monographs. 5:87–196.

Van Dierendonck, M. C., H. De Vries, and M. B. H. Schilder. 1995. An analysis of dominance, its behavioral parameters and possible determinants in a herd of icelandic horses in captivity. Neth. J. Zool. 45:362–385.

Veissier, I., V. Gesmier, P. Le Neindre, J. Y. Gautier, and G. Bertrand. 1994. The effects of rearing in individual crates on subsequent social behaviour of veal calves. Appl. Anim. Behav. Sci. 41:199–210.

Waran, N. K., N. Clarke, and M. Farnworth. 2008. The effects of weaning on the domestic horse (*Equus caballus*). Appl. Anim. Behav. Sci. 110:42–57.

Waring, G. H. 1983. Horse behavior. The behavioral traits and adaptations of domestic and wild horses, including ponies. Noyes Publications, Park Ridge, NJ.

Weeks, J. W., S. L. Crowell-Davis, A. B. Caudle, and G. L. Heusner. 2000. Aggression and social spacing in light horse (*Equus caballus*) mares and foals. Appl. Anim. Behav. Sci. 68:319–337.

Wells, S. M., and B. von Goldschmidt-Rothschild. 1979. Social behaviour and relationship in a herd of Camargue horses. Z. Tierpsychol. 49:363–380.