High-ranking mares of captive plains zebra *Equus burchelli* have greater reproductive success than low-ranking mares

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Abstract

Plains zebra live in harems that include one to six adult mares. Between these mares is a strong order of social hierarchy. The social rank of an equid mare is typically correlated with her age. Further, high-ranking captive plains zebra mares produce more surviving offspring than low-ranking mares. The objectives of this study were to, first, examined the factors that influence social rank of captive plains zebra mares, and second, test if high-ranking mares conceive earlier and if they have shorter inter-birth intervals than low-ranking ones. We observed three herds of captive plains zebra (a total of 18 mares) at the Dvůr Králové Zoo, Czech Republic. During the 831 h of observation, we recorded 1713 aggressive interactions (biting and offensive kicking) between the mares. These data were used to determine, for each mare, the total number of mares that dominated her in each period of social stability. The GLMM model revealed that older mares were dominated by a lower number of mares than the younger mares. We also found that the probability that a mare would conceive declined with the increasing number of dominant mares. Further, we tested the relationship between the number of dominant mares and the inter-birth interval using 29 intervals for 15 mares. These inter-birth intervals were divided into two groups. When a stallion was continuously present in the herd, the intervals lasted from one birth to the next birth (natural intervals). When a herd was without a stallion, the intervals lasted from the release of the stallion into the herd to the birth of foal (stallion-
influenced intervals). The analysis revealed that the inter-birth intervals decreased with an increasing number of dominant mares and the natural intervals decreased with an increasing number of offspring successfully reared by a mare. This finding is the first one in equids and contributes to the previous findings that suggest that social status influences reproductive success.

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1. Introduction

Plains zebra live in a family group (harem) consisting of a single breeding stallion and one to six adult mares (Klingel, 1964, 1967, 1969a,b; Monfort and Monfort, 1978; Hack et al., 2002). When young females are one to two and half of years of age and in oestrus, they are abducted from their families by other stallions (Klingel, 1967, 1969a). When a harem is formed, the females live in that harem for their entire life (Klingel, 1967). In the situation where a harem stallion dies, the harem remains intact and is taken over by another stallion (Klingel, 1967; Schilder, 1992).

Captive plains zebra have a very similar behavioural repertoire to wild plains zebra, as demonstrated in studies performed at both Danish and Dutch zoos (Andersen, 1992; Schilder and Boer, 1987). Further, plains zebra, mountain zebra (Equus zebra), domestic horses (E. caballus) and Przewalski horses (E. przewalskii) all have similar social systems, therefore, these species provide a useful comparison (Klingel, 1974, 1978; Rubenstein, 1993; Linklater, 2000).

There is a social hierarchy among the mares of both wild and captive plains zebra herds (Klingel, 1967; Schilder and Boer, 1987; Andersen, 1992). This hierarchy is mostly linear (Klingel, 1967; Schilder and Boer, 1987; Andersen, 1992). Despite this, the social hierarchy of plains zebra mares changes more often than the social hierarchy of mountain zebra and horses (Klingel, 1967; Joubert, 1972; Tyler, 1972; Berger, 1977; Wells and Goldschmidt-Rothschild, 1979; Schilder and Boer, 1987; Hogan et al., 1988; Kolter and Zimmermann, 1988; Lloyd and Rasa, 1989; Rasa and Lloyd, 1994).

The age of the mare seems to be the most important factor influencing the social rank of captive plains zebra (Andersen, 1992) and of feral and Przewalski horses (Tyler, 1972; Clutton-Brock et al., 1976; Wells and Goldschmidt-Rothschild, 1979; Carson and Wood-Gush, 1983; Keiper and Sambraus, 1986; Keiper, 1988; Klimov, 1988; Zharkikh, 1997; Sigurjónsdóttir et al., 2003; Rho et al., 2004). Lloyd and Rasa (1989) found that dominant mountain zebra females were older than the others in their group. Furthermore, there have been only a few horse researchers who have not found any positive correlation between the age of a mare and her social rank (Berger, 1977; Houpt et al., 1978; Haag et al., 1980).

Other researchers, using a different herd of horses, found that no clustering of pregnant mares near the top or the bottom of the hierarchy occurred. However, these same mares were not tested when they were not pregnant (Houpt et al., 1978). Further, it has been observed that wild females of the Hartmann zebra (E. z. hartmannae), a subspecies of mountain zebra, had no discernible influence on the social hierarchy of the herd during their gestation period (Joubert, 1972).
There are some reports that the birth (or presence) of a foal may result in a change of social hierarchy of equids, as suggested for the Cape mountain zebra (*E. z. zebra*; Penzhorn, 1979, 1984). These reports coincide with a recent finding that lactating wild plains zebra and feral horse females took more aggressive bites per minute than either pregnant or non-reproducing females or males (Neuhaus and Ruckstuhl, 2002; Rho et al., 2004). Contrary to these findings, other researchers found that horse mares with foals did not rank any higher in the hierarchies than mares without foals (Tyler, 1972; Keiper and Sambraus, 1986; Estep et al., 1993). Further, no changes in agonistic behaviour by new mothers were observed in two herds of domestic horses (Estep et al., 1993).

It is likely that social rank has the potential to influence reproductive success (equids: Schilder and Boer, 1987; Feh, 1988; Lloyd and Rasa, 1989; Rasa and Lloyd, 1994; other ungulates: Saharian arrui *Ammotragus lervia*—Cassinello, 1996, 2001; Cassinello and Alados, 1996; red deer *Cervus elaphus*—Clutton-Brock et al., 1984; Gomendio et al., 1990; Cuvier's gazella *Gazella cuvieri*—Alados and Escós, 1992). It has been observed that high-ranking captive plains and wild mountain zebra mares produce more surviving offspring than low-ranking mares (Schilder and Boer, 1987; Lloyd and Rasa, 1989). However, the captive plains zebra differed from the wild mountain zebra in terms of the sex ratio of their progeny. While the high-ranking mares of captive plains zebra tended to produce, in total, more surviving male offspring than the low-ranking mares (Schilder and Boer, 1987), the high-ranking mares of wild mountain zebra produced significantly more daughters than sons (Lloyd and Rasa, 1989).

Other researchers have reported that the offspring of dominant feral horse mares tended to be near the top of the hierarchy, while those of the middle- and low-ranking mares were not consistently found in the middle or bottom of their hierarchies (Houpt and Wolski, 1980). In studies on Camargue and domestic horses, researchers have found that the age of a foal tended to be related to its mother’s rank, since older, higher-ranking mares often foaled earlier (Wells and Goldschmidt-Rothschild, 1979; Araba and Crowell-Davis, 1994). Therefore, the social rank of a foal should be dependent on the social rank of its mother (Wells and Goldschmidt-Rothschild, 1979; Araba and Crowell-Davis, 1994). The reproductive success of Przewalski horses was found to be correlated with the rank of their mothers (Feh, 1988). Contrary to all of these findings, in a study on the horses of the Great Basin, no correlations between reproductive success and dominance were found (Berger, 1986). In that same study, only one female in the observed population retained alpha status in her band, and the number of foals she produced was no different than the three other females with whom she associated with for 4 years.

A high-ranking mare of captive plains zebra and horse has more access to food than low-ranking ones (Schilder and Boer, 1987; Rho et al., 2004). The differential access to provided food could play an important role in the zoos and safari parks (Schilder and Boer, 1987). Thus, the understanding of factors affecting social hierarchy could be important from the perspective of management as well as zoo welfare.

In the present study, we, first, analysed what variables influence the rank of a mare. Based on a majority of these previous findings, but not all, we predicted that the high-ranking captive plains zebra mares are those who (1) are older, (2) are pregnant, (3) have a dependent foal than the low-ranking ones. Second, we tested if the rank of the mare affected her reproductive success. Then, we predicted that (4) the probability of
conception decreases and (5) the inter-birth interval increases with decreasing rank of the mare.

2. Animals, materials and methods

2.1. Animals

We observed three herds of plains zebra during two seasons (from January 1999 to January 2000 and from September 2001 to March 2002, respectively) at the Dvůr Králové Zoo, Czech Republic. During the first season these herds contained seven, five and four mares, respectively, and during the second season they contained two, seven and four mares, respectively. A stallion was present in all but one herd (the herd with four mares during the second season). During both seasons there were some instances when a stallion was separated from its herd for several months for management purposes. Foals were present for the entire duration of both seasons in all of the observed herds.

The observed females aged from 18 months to 20 years. Those mares that were 18 months old were included in our sample since the first successful parturition in the study occurred in a female that was 31 months old. The gestation period of plains zebra is at least 361 days (Wackernagel, 1965; Lobanov, 1983). This meant that the mares we observed would have had their first successful estrus at the age of 19 months, which is the earliest age of successful conception recorded for plains zebra (compare: King, 1965; Wackernagel, 1965; Klingel, 1967, 1969a; Lobanov, 1983).

The size of the enclosures for the three herds were 1350, 800 and 1750 m², respectively. There was almost no vegetation present in any of the enclosures. Food was provided to the zebras ad libitum. They were given fresh food daily, usually in the morning. Ad libitum availability of food means that there were not any effects expected from lack of food in any time.

Each herd was observed at least once a week (on Saturday or Sunday—for technical reasons) during both seasons. We performed the observations in four different sessions each week. Each session lasted for 180 min, either from 08:00 to 11:00 or 14:00 to 17:00 h on Saturday or Sunday. We observed only one herd during each session (i.e. on Saturday morning we observed herd no. 1, in the afternoon herd no. 2, on Sunday morning herd no. 3 and in the afternoon again herd no. 1, the next Saturday we began with herd no. 2, etc.). In total, each of the three herds was observed for 315, 318, and 198 h, respectively.

2.2. Dominance

There is no consensus in the literature on how to measure the social hierarchy of equids (Wells and Goldschmidt-Rothschild, 1979; Keiper and Receveur, 1992; Estep et al., 1993; Van Dierendonck et al., 1995; Weeks et al., 2000). It has been reported several times that biting is the most frequent form of aggressive physical contact utilised by horse mares (Clutton-Brock et al., 1976; Berger, 1977, 1986; Wells and Goldschmidt-Rothschild, 1979; Houpt and Keiper, 1982; Carson and Wood-Gush, 1983; Keiper, 1988; Araba and Crowell-Davis, 1994). This behaviour has been successfully used in many
studies to determine the social hierarchy of equids. Further, it has been demonstrated that in herds of plains zebra and Asiatic asses, the individuals who had the highest biting frequency won all of the fights (Berger, 1981). Recently, Sigurjónsdóttir et al. (2003), in their study on domestic horses, showed that the measurements made by aggressive and submissive acts resulted in the same social hierarchy. In the present study, we recorded every case of biting and/or kicking among the mares and ignored any threats that were made. Since bites are typically directed towards subordinate animals and kicks tend to be used against dominant animals (Carson and Wood-Gush, 1983), we differentiated, according to the situation, between the types of kicking (i.e. defensive kicking and offensive kicking). Defensive kicking was identified and recorded when an animal kicked another animal after it had been chased to a corner and was sometimes bitten by the animal that it kicked. Offensive kicking was recorded when it occurred together with a biting during an offensive attack. For the purposes of this study, we only included the records of offensive kicking in the analysis.

For each herd, we divided each season into periods when the social hierarchy was stable: we recorded all possible mutual relationships among the herd members. The time boundary of the next period was defined as the time when a change in a dominance/subordinance relationship between any pair of individuals within the herd was detected. Once this happened, the next period started until the next change in the relationships occurred, etc. Then, based on dyadic interactions between mares, for each mare during each period, we estimated rank by a simple criterion of the number of mares who dominated her (further referred to as “number of dominant mares”).

2.3. Inter-birth intervals

Since the stallion was not present in each herd all of the time, we divided the inter-birth intervals into two groups. When the stallion was continuously present in the herd, then the intervals lasted from one birth to the next birth; we considered these as “natural intervals”. When the herd was without a stallion, the intervals lasted from the release of the stallion into the herd to the birth of foal; we considered these as “stallion-influenced intervals”.

2.4. Statistics

All data were analysed using the SAS System, Version 9.1. The relationships between the number of dominant mares, the age of the mare, her pregnancy status, if she had a dependent foal, and the sex and age of the foal were tested using a multivariate general linear mixed model (GLMM). In this model, the number of dominant mares was included as the dependent variable and all of the other factors described above were included as independent variables. To account for the repeated measures on the same individuals in the different herds and seasons, the analysis was performed using PROC MIXED, with the identity of the mare, nested within the herd, interacting with the season (herd × season) included as a random factor. The significance of each fixed effect in the mixed GLMM was assessed using an F-test. We started with the full model including all of the fixed effects and sequentially dropped those effects which were not significant. The independent variables consisted of both class variables (‘pregnancy of the mare’—
yes during the whole period, yes during a part of the period or no; ‘if she had a foal’—yes during the whole period, yes during a part of the period or no; ‘if she had a dependent foal’—yes during the whole period, yes during a part of the period or no; ‘sex of a foal’—male or female; ‘presence of kin adult mare in the herd’—mother, daughter or nobody) and continuous variables (‘age of the mare at the end of the period’ ranging from 642 to 7013 days, ‘age of the dependent foal at the end of the period’ ranging from 26 to 421 days, ‘number of mares in the herd’ ranging from 3 to 7, ‘number of previous births’ ranging from 0 to 14 births and ‘number of offspring successfully reared by the mare’ ranging from 0 to 11 offspring). The sex and age of the foal were nested within whether the mare had a dependent foal or not. Since this was an unbalanced design, with more than one effect, the arithmetic mean for a group did not accurately reflect the response for that group, since it did not take into account the other effects. Therefore, we used the least-squares-means (LSMEANs). LSMEANs are, in effect, within-group means that are appropriately adjusted for the other effects in the model. LSMEANs (further referred to as ‘adjusted means’) were computed for each class variable. The differences between the classes were tested by $t$-test. For multiple comparisons we used the Tukey–Kramer adjustment.

To assess the impact of number of dominant mares on successful conception of the mare, we applied an analysis of categorical repeated measurements based on the generalized estimating equation approach (Liang and Zeger, 1986) using the GENMOD procedure. The GENMOD procedure was designed to model the probability that the mare conceives. To account for the repeated measures on the same individuals across the period of observation, the analysis was performed with the individual mare, nested within the herd, as a SUBJECT in the REPEATED statement. The explanatory variables were: the number of dominant mares (at the date of foaling), the identity of the mare and the herd, the season, the mare’s age, the number of mares in the herd, the number of previous births, and the number of offspring successfully reared by a mare (as independent variables). Both explanatory variables and the interaction term were tested, but are not reported unless they were statistically significant ($P < 0.05$).

We then analysed the association between the inter-birth interval (as a dependent variable) and the type of interval (natural or stallion-influenced interval), the number of dominant mares (at the date of foaling), the identity of the mare and the herd, the sex of the dependent foal, the sex of the foal not yet born, the mare’s age, the identity of the stallion, the number of previous births, and the number of offspring successfully reared by a mare (as independent variables). We analysed these variables using a GLMM, treating the identity of the mare, nested within the herd, as a random factor.

Relationships between the number of dominant mares, the mare (or the inter-birth interval), and the other variables were estimated by fitting a random coefficient model using PROC MIXED, as described by Tao et al. (2002). The fixed effects included in the model were number of dominant mares and ‘inter-birth intervals’; the SUBJECT in the model was the ‘identity of the mare, nested within the herd interacting with the season’. With this random coefficient model we calculated the predicted value of the number of dominant mares for each mare and plotted this against the age of the mare (we also plotted the predicted value of the inter-birth interval against the number of dominant mares) using a predicted regression line.
3. Results

In total, we recorded 1713 offensive attacks (1540 bites and 173 kicks) during the 831 h of observation (277 sessions during 159 days). In the first season the social hierarchy changed once, twice and four times, respectively, in the three observed herds. In the second season, the social hierarchy remained stable in all three herds. Thus, for the entire study, we recorded 13 periods of social stability. For all of these periods combined, we calculated 68 records in which a mare was either the most dominant or was dominated by one or more other mares.

In the first GLMM analysis, the final model contained two fixed effects (age of the mare and the number of mares within the herd). The number of dominant mares to the mare was significantly related to the age of the mare ($F = 6.51$; d.f. = 1, 55.8; $P = 0.004$); the older mares were dominated by a smaller number of mares than the younger ones (Fig. 1). With a
smaller herd size, the number of dominant mares was logically lower ($F = 9.67; \text{d.f.} = 1, 29.6; P = 0.014$).

In the second model, we analysed only those mares, which were not pregnant in the beginning of the period. Therefore, this left only 8 of the 13 periods. Fifteen individual mares were used in this analysis, with some of them entered the analysis more than once. In 12 cases, the mare conceived successfully during the period, while in 11 cases, the mare did not conceive during the period. The GLMM revealed that the successful conceptions within the period decreased with an increasing number of mares who dominated the focal mare ($F = 4.44; \text{d.f.} = 1; P = 0.035$, Fig. 2).

For the last GLMM model, we analysed the 11 natural inter-birth intervals and the 18 stallion-influenced intervals collected from the 15 different mares in the three herds. In both cases, the mares dominated by a smaller number of mares had shorter intervals than

Fig. 3. The relationship between the inter-birth intervals and the number of dominant mares.

Fig. 4. The predicted length of the inter-birth intervals according to the sex of the following foal and according to the type of interval. The values are adjusted means ($\pm$S.E.).
the mares dominated by a higher number of mares \((F = 3.53; \text{d.f.} = 2, 29; P = 0.043; \text{Fig. 3})\). The inter-birth interval was also affected by the sex of the foal that was not yet born \((F = 8.81; \text{d.f.} = 3, 29; P = 0.003)\). There was a tendency for longer natural inter-birth intervals when the foal that was not yet born was a male. Detailed differences did not reach significance \((P < 0.07, \text{Fig. 4})\). We also found that the intervals decreased with an increasing number of offspring successfully reared by a mare \((F = 13.27; \text{d.f.} = 2, 29; P < 0.001; \text{Fig. 5})\). This was true for natural inter-birth intervals (Solution for fixed effects, \(t = -5.08, \text{d.f.} = 29; P < 0.0001\)), but not for stallion-influenced intervals (Solution for fixed effects, \(t = -0.85, \text{d.f.} = 29; \text{NS}\)). The stallion-influenced intervals were shorter than the natural inter-birth intervals (see Figs. 3–5).

4. Discussion

In this study, we found that the age of the mare affected her social rank. This finding is in agreement with various reports that dealt with harem-living zebras (Lloyd and Rasa, 1989; Andersen, 1992) and horses (Tyler, 1972; Clutton-Brock et al., 1976; Wells and Goldschmidt-Rothschild, 1979; Carson and Wood-Gush, 1983; Keiper, 1988; Keiper and Sambraus, 1986; Klimov, 1988; Zharkikh, 1997; Sigurjónsdóttir et al., 2003; Rho et al., 2004). Further, it has been reported that the rank position of a domestic horse mare was positively correlated with her age and with the residency time of the mare in the herd (Van Dierendonck et al., 1995). Older females could have a higher rank, not directly because they are older, but because they inevitably have been in a group longer than the low-ranking mares. It is possible that the longer a mare is in a group, the higher up the dominance “ladder” she progresses. Dominance rank could be related directly to residency time in the group, such that ranks function like a queue. Therefore, dominance rank could be indirectly related to age via the greater time that an animal has had an opportunity to be in a group. All of the females observed in this study had been in the same herd since they were born; therefore, we were unable to distinguish between the effect of age and residency time.
We did not find any evidence for a possible effect of pregnancy on dominance ranking. This same result has been reported for both wild Hartmann mountain zebra and horses (Joubert, 1972; Berger, 1977; Houpt et al., 1978). On the other hand, other researchers, such as Houpt et al. (1978), have suggested that pregnancy could influence the rank of domestic horse mares. The influence of oestrus on social hierarchy has been documented only once in a study on wild Cape mountain zebra (Penzhorn, 1979, 1984).

Similarly, we did not record any change in the social hierarchy (measured by the number of dominating mares) after foaling. This corresponds with the findings of other horse researchers (Tyler, 1972; Keiper and Sambraus, 1986; Estep et al., 1993). It has been also previously been reported that after foaling, mothers defended their foals from other members of the herd; despite this, the rank position of the mothers did not change (compare with: Klingel, 1969a; Estep et al., 1993).

The probability of conception depended on the number of dominant mares, but not on the number of herd members. With an increasing number of dominant mares, the probability of the mare to conceive declined. This could be due to various kinds of stressful activities from high-ranking mares, e.g. interventions of high-ranking mares into copulations of low-ranking ones. We recorded only one intervention during copulation. A mare, which had successfully conceived during the previous period and had changed her rank with an older mare, intervened and interrupted copulation of the older mare. The mare prevented from copulation did not conceive for several months. Schilder (1990) observed in his study on captive plains zebras several cases of interventions during copulations. However, he did not find that dominance played a role in the interventions. In seasonal reproducing species, like the feral horse, higher-ranking mares tended to have older foals than the lower-ranking ones (Wells and Goldschmidt-Rothschild, 1979).

The inter-birth interval appeared to be affected by the number of dominant mares. It was typically shorter for those mares that were dominated by a smaller number of mares. Such mares gave also birth earlier after the introduction of a stallion into the herd. In the wild, as in the captivity, births do occur in each month of the year (Wackernagel, 1965; Klingel, 1969a,b; Smuts, 1976; our unpublished data). In the captive plains zebra mare, the first oestrus typically occurs 7–9 days after parturition (Wackernagel, 1965). Thus, when a stallion was continuously present within the herd, high-ranking mares could improve their reproductive success by higher number of offspring produced due to shortening their inter-birth intervals. When the stallion was introduced into the herd, high-ranking mares could improve their reproductive success by giving birth sooner than the low-ranking ones. In this case, the older foals of high-ranking mares would suffer less by predation in the presence of the younger foals of low-ranking mares than the younger ones would.

Shorter inter-birth intervals of high-ranking females in comparison with low-ranking females have been observed for several primates, such as macaques Macaca mulatta (Nevison et al., 1996), baboons Papio cynocephalus (Smuts and Nicolson, 1989; Packer et al., 1995) or chimpanzees Pan troglodytes (Pusey et al., 1997; for a review see Ellis, 1995). As we are aware, similar results to this were reported for one ungulate population only, captive Saharan arrui (Cassiniello and Alados, 1996). On the other hand, other researches have found that the inter-birth intervals of dominant and subordinate wild mountain zebra mares, who do not reproduce seasonally, were equal and independent of age (Lloyd and Rasa, 1989; Rasa and Lloyd, 1994). However, due to small sample size used
by these researchers, the lack of significant difference between the dominant and subordinate individuals does not fully prove that there was no difference. Thus, as we are aware of, our finding is the first one among equids and second one among ungulates. This could be due to the fact that the most of the investigated ungulate species live in temperate zones and reproduce seasonally.

We found a tendency for the natural inter-birth intervals to be longer when mares conceived male progeny compared to when they conceived female progeny. This trend was not seen in the stallion influenced intervals. This could imply that mares invest more into male progeny than into female offspring, especially in cases where they have a suckling foal. This thought is in accordance with a sociobiological theory about differential investment into males and females in polygynous mammals (Clutton-Brock et al., 1981), and with results that indicated a tendency for feral horse mares to conceive males after a longer period of time than females (Cameron et al., 1999). Another explanation of longer inter-birth intervals for male progeny could be that male foals take a few days longer to develop physiologically than female foals. Then, a difference of pregnancy length between male and female progeny should take place. Moreover, the indication for such a difference was reported for captive plains zebras (Wackernagel, 1965).

We also found that the length of the inter-birth interval decreased with an increasing number of previous successfully reared offspring. For several seasonal reproducing ungulate species it has been reported that the older females improve their reproductive success by giving birth in each reproductive season (feral horse—Cameron et al., 2000, bighorn sheep Ovis canadensis—Festa-Bianchet, 1988). We also included the age of mare and the number of births into our analysis. However, we did not detect any influence of these factors on the inter-birth intervals. Our study was on a captive population, thus we have exact data concerning the number of births and successfully reared offspring for each mare that we tested. It is very difficult to obtain such data in studies dealing with wild populations. As we are aware, our finding is unique among ungulates.

Our results suggest that the stallion-influenced intervals were generally shorter than the natural intervals. This is due to the fact that, in stallion-influenced intervals, the mares do not care for a foal and they could conceive without any delay.

In wild plains zebra, the social hierarchy of the females is not stable in time, and may change as often as once a month (Klingel, 1967). Nevertheless, this same researcher showed that the social hierarchy of a marked group of wild plains zebra stayed the same for almost a year. There was at least one change in the social hierarchy during the first season in each of the captive herds that we observed. However, no changes in hierarchy were observed during the second season. Most of the observed changes that occurred in the first season were prompted by the introduction or the removal of animals, particularly the stallions. Having a stable social hierarchy among mares is quite common for wild mountain zebra (Joubert, 1972; Rasa and Lloyd, 1994). During a long-term study (20 years), researchers only observed one incidence where a dominant mare was supplanted by a subordinate mare (Lloyd and Rasa, 1989; Rasa and Lloyd, 1994). It has been reported by various researchers that in many horse populations dominance remains stable and the rankings of the horses do not change over time (Tyler, 1972; Berger, 1977; Wells and Goldschmidt-Rothschild, 1979; Kolter and Zimmermann, 1988). Conversely, it has been observed that the hierarchy of a horse population changed within 3 years (Keiper and
Further, it has been observed that dominance relationships in the Great Basin’s horse population changed regularly, and most often over periods that spanned a few days to several weeks (Berger, 1986). Therefore, it seems that the stability of social hierarchy of captive plains zebra mares is similar to that reported in horses.

An understanding of the pattern of dominance in captive ungulates and its effects could be helpful to management systems (Seror et al., 2002; Wirtu et al., 2004). Thus, we hope that our findings could contribute to better management and welfare of captive plains zebras.

5. Conclusion

In agreement with other studies on plains and mountain zebra, and the Przewalski horse (Schilder and Boer, 1987; Feh, 1988; Lloyd and Rasa, 1989; Rasa and Lloyd, 1994), we can conclude that age determines the rank of the captive plains zebra mare. We also found that high-ranking captive plains zebra mares can improve their reproductive success by shortening their inter-birth intervals due to either earlier successfully conception after parturition or the introduction of a stallion.

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