

Gender Differences in Maternal Intervention in Jeju Ponies (*Equus caballus*)

Rho, Jeong R., Robert B. Srygley¹ and Jae C. Choe^{2*}

Division of Research, Seoul Grand Park Zoo, Gwacheon 427-702, Korea

¹Smithsonian Tropical Research Institute, Apdo. 2072, Balboa, Republic of Panama

²Laboratory of Behavior and Ecology, School of Biological Sciences, Seoul National University, Seoul 151-742, Korea

ABSTRACT: We investigated interventions by mother Jeju ponies on Jeju Island, Korea, to determine whether mothers assisted their offspring to attain higher status within the dominance hierarchy. Because dominance rank is important within each gender, we predicted that mothers would be more likely to intervene when their foals were play-fighting with foals of the same gender. A total of 173 play-fighting events were recorded from March to October 1998 and from April to October 1999. Of these, foals were more likely to play-fight with a foal of the same gender as with a foal of the opposite gender (120 versus 53 occurrences, respectively). A mother of one of the foals that were play-fighting intervened in 17 of these interactions. Contrary to the prediction, a mare was more likely to intervene when opposite genders interacted than when the same gender interacted. Analyzing interactions between the opposite genders further, mothers were equally likely to intervene when a daughter was play-fighting with a male foal as when a son was play-fighting with a female foal. Hence, mothers were not more protective of daughters than sons. Mothers that were in the younger age class (2~11 years old) were as likely to intervene as those in the elder age class (17~25 years old). However, all foals that were harassed were offspring of mothers in the younger, more subordinate age class. Intervention directly maintains the dominance rank of the intervening mother, and may indirectly assist the intervening mother's foal to achieve a higher dominance rank. By discouraging their foals from play-fighting with the opposite genders, dominant mothers may be encouraging their foals to play-fight with the same gender and participate in establishing its own dominance rank.

Key words: *Equus caballus*, Helping behaviour, Intervention, Jeju pony, Play-fighting

INTRODUCTION

Dominance ranks of daughters are correlated with those of their mothers in some ungulate species (Saharan arrui *Ammotragus lervia sahariensis*, Cassinello 1995, mouflon sheep *Ovis gmelini*: Guilhem *et al.* 2000). In horses (*Equus caballus*), dominance ranks of foals, both before and after weaning, were positively correlated with the rank of their mothers (Araba and Crowe-Davis 1994). The foals of dominant mares tend to be dominant in their own age groups (Haupt and Wolski 1980) and also dominant when compared to foals of subordinate mares within the herd (Haupt *et al.* 1978). Haupt *et al.* (1978) reported that a foal's rank was positively correlated with its total aggression. Weeks *et al.* (2000) also reported that foals of higher-ranked mares had higher rates of giving aggression and received less aggression than foals of lower-ranked horses.

Several possible mechanisms of inheritance of maternal rank have been proposed. One hypothesis is that inheritance of maternal rank is due to phenotypic similarities between mothers and daughters that result from genetically determined traits. A second hypothesis is that

inheritance of dominance hierarchy resulted from the foals learning aggressive behaviour from their parents (Haupt and Wolski 1980). A third hypothesis is that parents intervene or assist offspring, regardless of the offspring's sex, to gain higher dominance rank. Weeks *et al.* (2000) observed that more dominant mares were within close proximity to their foals relative to more subordinate mares, leading to their suggestion that mares may aid their foals in agonistic encounters with peers of the same age. Hence, a more dominant parent is more likely to be able to assist its offspring. Consequently, offspring rank becomes similar to maternal rank.

It is well established that interventions have a short-term consequence of increasing or decreasing the likelihood that two individuals will interact. In zebra (*Equus burchelli*) interventions are frequent and serve to prevent or hinder two other individuals from interacting (Schilder 1990). In ponies (*Equus caballus*), mothers sometimes intervene to protect their foals when threatened by yearlings or other foals (Tyler 1972).

However, the longer-term functional consequences of intervening between two individuals have been less explored. There are some examples of intervention-based rank inheritance among primates,

* Corresponding author; Phone: +82-2-880-8157, Fax: +82-2-882-7195, e-mail: jcchoe@snu.ac.kr

including baboons (Hausfater *et al.* 1982) and vervet monkeys (Horrocks and Hunter 1983), but none are known in ungulates.

The proximity of mares to their foals suggests that they could intervene to assist the foals' in dominance interactions. In Welsh ponies, for example, Crowell-Davis (1986) observed that a mare and her foal spent at least 50% of the time within 5 m of each other through week 2. In horses, mothers cared for their foals more frequently when in close proximity (Waring 1983). Mothers intervened when their foals were play-fighting with other foals or to protect their foals from aggressive encounters (Waring 1983). Play-fighting was observed frequently in the early stage of a foal's life (Tyler 1972, Waring 1983), but no one has investigated whether foals might be more likely to win the play-fighting by intervention from their mothers. Moreover, details are lacking on the gender of foals that play-fight, and its role in eliciting intervention by their mothers during the early life of the foal.

Here with a case study of the Jeju pony, we explore whether the parental intervention observed in ungulates might help the offspring to obtain a higher dominance rank. We investigate the hypothesis that mothers intrude to help their offspring dominate over their peers and thus help them in future encounters to move up the social dominance hierarchy. Because dominance hierarchies are important within each gender, we predicted that mothers would intervene more often when offspring were play-fighting with foals of the same gender. Second, because dominance of mares is associated with age in our focal animal (Rho 2002), we predicted that older, and presumably more dominant, mothers would be more likely to intervene than younger, less dominant mares.

MATERIALS AND METHODS

Study Site and Subject

The study was conducted on a herd of ponies on Jeju Island (33°25'50" N, 126°36' E), Korea. The herd was first established in 1986 with 64 mares and 1 stallion and has been maintained at a similar size by the Institute for Livestock Promotion. The herd size of the farm has usually been maintained at 45~73 mares, their foals and one stallion since 1986.

The farm consists of a fenced-in 233 ha grassy area interspersed with tall trees. The herd feeds on grass from April to October since 1986 (from March to October as of 1998). Water is always available at an artificial drinking station. Food was usually abundant from April to October on the grass, but was slightly less abundant during the wet season (during June, as of 1988). The pasture has been maintained in a good condition throughout the existence of the colony. In winter during and following heavy snowfall, the herd is transferred to a pasture behind a barn and provided with hay and con-

centrated feed. There is a grassy area of about 4 ha behind the barn. The mares rest, play, or graze in the grassy area during winter.

The mares in the herd comprise the mares introduced in 1986 plus those born on the farm. The farm keepers in the Jeju Province Institute for Livestock Promotion have maintained an accurate record of life history parameters such as birth date and genetic relationships among members of the herd since 1986. The farm keepers also checked and recorded all signs of illnesses or injuries each day in the early morning. If a mare was ill or injured, it was excluded from the herd and treated immediately with the aid of a veterinary surgeon, and then it was either reintroduced or reared individually in a barn until December.

Between 23~53 foals were born every year since 1987. Of these, approximately 2~5 yr old foals were kept and the remainder were sold at an auction in December every year. Some healthy mares along with the seriously diseased, ill or injured mares were also sold at the auction to maintain a consistent herd size.

Stallions were kept isolated from the herd in the Jeju Province Institute for Livestock Promotion. Each year, a single stallion was introduced into the herd. In order to avoid inbreeding between a father and his daughters, the stallion in the herd was exchanged for another stallion each year. When a stallion was newly introduced, if the possibility of inbreeding existed, his daughters, mothers, and grand-mother were transferred out and sold at the auction.

There were 73 mares and 53 yearlings in 1998, and 72 mares and 41 yearlings in 1999. The mares that ranged in age from 2 to 11 years were born on the farm. Fourteen additional mares were part of the initial herd. Their ages were estimated in 1986 based on the degree of tooth wear (accurate to ± 1 year, Ensminger, 1969). At the time of this study, these mares, ranging from 17 to 25 years of age, composed an elder group. In a related study, we found that dominance rank in female Jeju ponies is linear, and a mare's dominance rank increased with age (Rho 2002, Rho *et al.* 2004).

The herd consisted of some sub-groups, although they lived in one herd. The members in each sub-group ranged from 2 to 5 mares. The ages of the mares in the same sub-group were usually similar. Sub-group members tended to group together when moving, grazing, resting and sleeping. The members in each sub-group were sometimes exchanged with mares in another sub-group before or after parturition during our study. There were, however, three sub-groups for which the members never changed during our study. The mares in these three sub-groups were over 19 years old.

Data Collection

The first author (JRR) collected the data from March to October 1998 and from April to October 1999. Observations were made during daylight (between 07:00 and 19:00 h) using the focal animal

continuous sampling method (*sensu* Altmann 1974). Diurnal activity pattern of Jeju pony mares varies across both months and from day to day (Rho and Choe 2002). Thus, the daily observation was divided into four 3-hour periods: 07:00~10:00 h, 10:00~13:00 h, 13:00~16:00 h, and 16:00~19:00 h. JRR tried to conduct observations in different time periods on different days to sample equally across all time periods. When it was very rainy or a foggy day, JRR did not observe the mares and their foals.

Data for this study were collected for 50 mares and their foals aged 4 (N=26), 7 (N=38), 14 (N=49), 30 (N=48), 60 (N=38), 90 (N=37), and 120 (N=33) days. (Foal age classes are accurate to ± 2 days, except for the 4 and 7 day old foals. In these, age is accurate to ± 1 day.) JRR tried to conduct observations of the same mares and foals as their foals aged.

JRR identified all individual ponies which interacted by distinctive markings on their backs and other body characteristics such as general body shape, coat color, etc. The sampled mares and their foals were usually observed on foot without disturbance from about 25~30 m by the naked eyes. We considered harassment, if a foal was threaten and kicked or bitten by a mare. Data collected when the ponies were disturbed by the pony managers or park visitors were not used in the analyses.

Data Analyses

We analyzed 220 play-fighting interactions. We tested the prediction that mothers intervene more frequently when their foals were play-fighting with a foal of the same gender and less often when play-fighting with the opposite genders by counting observations of each and comparing those for which a mother intervened to those for which a mother did not intervene. Deviations from the null hypotheses were analyzed statistically with Chi-square test. If the same pair of foals were play-fighting more than once, then we selected one of the events at random and excluded the others from the analyses (47 events were excluded).

Because of the gap in their ages, mares fell naturally into two age classes: Older mares (17~25 years old) and Younger mares (2~11 years old). We applied a Chi-square test whether the age class of the mothers effected the harassment of their foals. To determine whether mares that were mothers of harassed foals were younger than the mare that intervened, we applied a binomial test.

RESULTS

We accumulated 658 hours of observation in 1998 and 1999 on 50 mares and their foals. A total of 173 play-fighting interactions between different foals were recorded during the observation period. Fig. 1 illustrates the proportion of play-fighting in the foals who

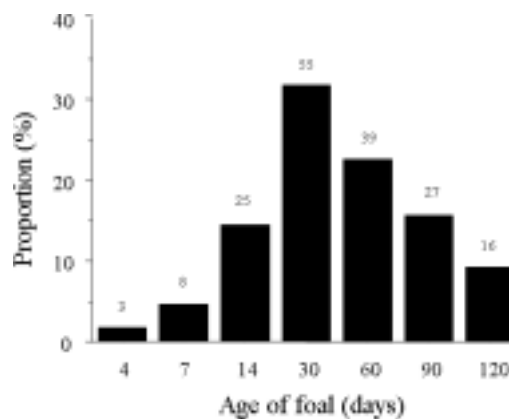


Fig. 1. The proportion of play-fighting foals that were between 4 and 120 days old. The number of foals that were play-fighting is indicated over each bar of the histogram (N=173).

were from 4 to 120-day old. Play-fighting was most common among foals that were 30~60 days of age. The foals were play-fighting with a foal of the same gender (N=120, 69.4%) more than twice as often as with one of the opposite genders (N=53, 30.6%). For play-fighting between foals of the same gender, 97 play-fighting events were between male foals and 23 were between female foals. During the 173 play-fighting interactions, a total of 17 maternal interventions by 17 different mares were recorded. When threatened, the foal which was not an offspring tried to avoid the intervening mare, and ran further away when kicked or bitten. Of the 17 interventions, ten were threat displays, and seven escalated to bites, which in some instances, were followed by kicks.

Mothers intervened more frequently toward their foals who were play-fighting with opposite genders (Fig. 2, N=9 interventions of 53 events, 17%) than with same gender (N=8, 6.7%, Chi-square

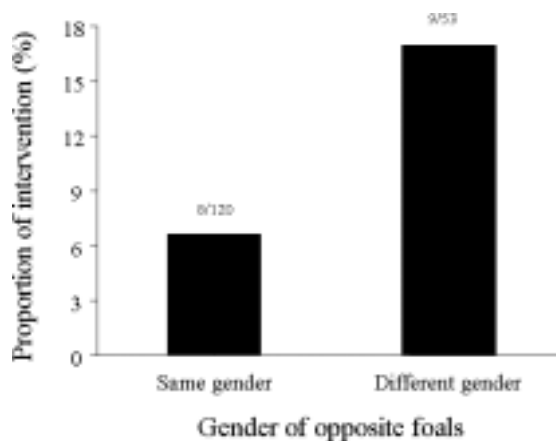


Fig. 2. The proportion of the mares' interventions in play-fights between their offspring and foals of the same gender or opposite genders. Fractions indicate the frequency of maternal interventions divided by the number of play-fighting events in each category.



Fig. 3. Age of the harasser relative to the age of the harassed foal's mother. The fractions indicate the frequency of interventions by a mother in each age class divided by the total number of interventions.

test, $\chi^2=4.41$, $df=1$, $p=0.036$). A mother was equally likely to intervene when its daughter was play-fighting with a male foal ($N=5$, 16%) than when its son was play-fighting with a female foal ($N=4$, 19%, Chi-square test: $p=0.75$). These results are contrary to our prediction that mares are intervening specifically to assist their offspring to obtain a higher dominance status among their peers.

The proportion of the observed intervention was 6.9% ($N=6$) in the play-fighting between the foals produced by the younger age class, 13.3% ($N=10$) between the foals produced by the younger and older age class, and 8% ($N=1$) between the foals produced by the older age class (Chi-square test, $p=0.39$). In the 17 interventions, the intervening mothers were significantly older than the mothers of the foals who were harassed (Binomial test that mares were older relative to equal in age or younger: $p=0.047$). Of the 17 interventions, 12 (70.6%) of the mares who intervened were older, 3 (17.6%) were younger, and 2 (11.8%) were of the same age as the mother of the other foal. Hence, dominance plays an important role in the probability of intrusion. Foals of mares that were subordinate were more likely to be intruded upon when play-fighting. Therefore, intervention directly maintains the dominance rank of the intervening mother, and may indirectly assist the intervening mother's foal to achieve a higher dominance rank.

DISCUSSION

Dominant mothers are more likely to intrude on the foals of subordinate mares. This action serves to maintain or enhance the dominance of the intruding mare. Moreover, when the foals are the same gender, this behaviour may enhance the dominance of the foal of the intruding mare. However, contrary to our prediction, mares were more likely to intrude on foals when the two were of opposite

genders than when they were of the same gender. By discouraging their foals from play-fighting with the opposite genders, dominant mothers may be encouraging their foals to play-fight with the same gender and participate in establishing its own dominance rank.

In our results, play-fighting between foals began at 4-day old, and was most common among foals between 30~60 days of life. Tyler (1972) first observed social play between foals during the first week of a foals' life. After 3 to 4 weeks of life, the social attachments between mothers and their foals decreased, and those between foals or yearlings became more numerous. The results of Crowell-Davis (1987) were similar with the results of Tyler (1972). We also suppose that Jeju foals begin to relate socially between peers of the same age and pursue higher ranks in the dominance hierarchy from 2~4 weeks of life.

Dominant mothers are more likely to intrude on the foals of subordinate mares. Intervention ceased the social interaction and mares frequently harassed the foal that was play-fighting with its offspring. Such interventions were directed at foals of younger mares. This action serves to maintain or enhance the dominance of the intruding mare. Thouless and Greenberg (in red deer, 1986) and Rutberg (in bison cows, 1983) noted that dominance ranks were affected by previous agonistic experiences. An individual was more likely to win if it had previously met and defeated its opponent in an agonistic encounter. For Jeju ponies, this suggests that a mother's intervention increases the probability that her foal will win future encounters. The foal probably becomes more vigorous and likely to dominate over a peer.

Moreover, when the foals are the same gender, this behavior may enhance the dominance of the foal of the intruding mare. The intervention by mothers when foals of the same gender interact may increase the rank of their offspring in the dominance hierarchy. The dominance hierarchy is typically established among males or females within the herd. Reproductive success increases with dominance rank for males (Feh 1999) and with age for females (Cameron *et al.* 2000). Because dominance rank increased with age in Jeju ponies (Rho 2002), we presume that reproductive success also increases with dominance rank. A longer-term field study is needed to confirm this.

Contrary to our prediction, however, mares were more likely to intrude on foals when the two were of opposite genders than when they were of the same gender. We have found that mothers did not always intervene to directly increase the dominance rank of their foals amongst peers of the same gender in Jeju ponies. These results suggest that interactions between different genders are important, and mothers interfere in the social interactions between opposite genders. Mothers may intervene to help their foals, to cease the social interaction, or to threaten the opposing foals when play-fighting.

In a related study of Jeju ponies (Rho unpublished data), the frequency of grooming between foals that were 14 to 120 days old was dependent on the genders of the foals. Male and female foals were more likely to groom one another (52% of the 73 events) than groom a foal of the same gender. Females were less likely than males to groom one another (16% relative to 32%). Tyler (1972) and Waring (1983) also found that interactions between opposite genders were more common than between male or between female foals. The results imply that social interactions begin between male and female foals at early stage of life. Waring (1983) and Crowell-Davis (1987) also suggested that at adolescence, social contacts between opposite genders increased, and they interpret these interactions as sexual behaviour. In Jeju ponies, mothers were more likely to intervene when their offspring were play-fighting with a foal of the opposite genders than when the foals were play fighting with a foal of the same gender. This suggests that the male or female foals may be establishing or maintaining their social relation with the opposite genders to be ensured of future reproductive benefits. In addition, when a mare intervened between individuals of the same gender, she may have partly influenced the dominance of her offspring.

For Jeju ponies, mothers were as likely to intervene when their sons were play-fighting with a female foal as when their daughters were play-fighting with a male foal. Mothers may be assisting sons to win play-fights, whereas they may be intruding on daughters to cease play-fighting. The ability of a male to attract females usually depends on its dominance. Winning play-fights over female foals may be one means by which she assesses the male foal's dominance and future success as a leader of a herd. Mothers may discourage daughters from interacting with male foals because the daughter's participation in a group of exclusively young stallions will, on average, reduce her reproductive success relative to that if she joins a harem that consists of older stallions (Linklater *et al.* 1999, Davies Morel and Gunnarsson 2000). If it is true that mothers are intruding to assist sons to dominate over females but discourage daughters from play-fighting with males, then mothers should be willing to escalate the intrusion when daughters are play-fighting with male foals more often than when sons are play-fighting with female foals. We do not have sufficient data to address this prediction currently, but the data are in the predicted direction. When intruding on a daughter play-fighting with a male foal, the mare escalated from threat to bite in three cases out of five; whereas when intruding on a son, the mare escalated in only one case out of four.

For Jeju ponies, dominant mothers are more likely to intrude on the foals of subordinate mares. As a result, more dominant mothers assist their foals in social interactions. Social experience of sons will

later influence the age at which the pony acquires a harem. Evidence from horses suggests that males that interacted with females prior to maturation were more advanced in obtaining a harem than those that did not interact with the herd (Khalil and Kaseda 1998). In addition, social experience of daughters will later influence the ponies' options to join a harem. Therefore, we suggest that mothers assist their foals to join a group that will enhance the foals' reproductive success.

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