OPEN ACCESS Freely available online

PLoS one

Adult-Young Ratio, a Major Factor Regulating Social Behaviour of Young: A Horse Study

Marie Bourjade[1,2]*, Alice de Boyer des Roches[1], Martine Hausberger[1]

1 Université de Rennes 1, Laboratoire d'Ethologie Animale et Humaine, Centre National de la Recherche Scientifique, Rennes, France, **2** Association Takh pour le cheval de Przewalski, Station Biologique de la Tour du Valat, Arles, France

Abstract

Background: Adults play an important role in regulating the social behaviour of young individuals. However, a few pioneer studies suggest that, more than the mere presence of adults, their proportions in social groups affect the social development of young. Here, we hypothesized that aggression rates and social cohesion were correlated to adult-young ratios. Our biological model was naturally-formed groups of Przewalski horses, *Equus f. przewalskii*, varying in composition.

Methodology/Principal Findings: We investigated the social interactions and spatial relationships of 12 one- and two-year-old Przewalski horses belonging to five families with adult-young ratios (AYR) ranging from 0.67 to 1.33. We found striking variations of aggression rates and spatial relationships related to the adult-young ratio: the lower this ratio, the more the young were aggressive, the more young and adults segregated and the tighter the young bonded to other young.

Conclusion/Significance: This is the first study demonstrating a correlation between adult-young ratios and aggression rates and social cohesion of young individuals in a naturalistic setting. The increase of aggression and the emergence of social segregation in groups with lower proportions of adults could reflect a related decrease of the influence of adults as regulators of the behaviour of young. This social regulation has both theoretical and practical implications for understanding the modalities of the influence of adults during ontogeny and for recommending optimal settings, as for instance, for schooling or animal group management.

Citation: Bourjade M, de Boyer des Roches A, Hausberger M (2009) Adult-Young Ratio, a Major Factor Regulating Social Behaviour of Young: A Horse Study. PLoS ONE 4(3): e4888. doi:10.1371/journal.pone.0004888

Editor: Martin Giurfa, Centre de Recherches su la Cognition Animale - Centre National de la Recherche Scientifique and Université Paul Sabatier, France

Received November 25, 2008; **Accepted** February 15, 2009; **Published** March 18, 2009

Funding: The Association Takh was supported financially by the MAVA foundation but this work did not receive specific funding. The funder had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

* E-mail: marie.bourjade@gmail.com

Introduction

Evidence of the vast role played by human adults and adults of some animal species in regulating the social behaviour of young is now widespread [1,2]. Experienced adults can be essential in providing models for learning behaviour socially (e.g. response of young to novel food: lambs, *Ovis aries* [3], common marmosets, *Callithrix jacchus* [4]) and above all, as models for producing and using adequate social signals efficiently [1,5,6]. For example, young brown-headed cowbird males, *Molothrus ater*, raised without adults were able to produce potent songs, but were unsuccessful when courting females because they failed to direct songs towards females and formed less consortships than males raised with adults [7,8]. The absence of adults also affects language development of human children, *Homo s. sapiens*, and associates with externalizing problems in human adolescents [9,10].

Such deleterious effects on the development of social behaviour due to the absence of adults have been widely reported in songbirds (e.g. brown-headed cowbirds [8,11], European starlings, *Sturnus vulgaris* [12]) and, to a lesser extent, in mammals (e.g. African elephants, *Loxodonta Africana* [13], domestic horses, *Equus ferus caballus* [14]). Indeed, direct evidence shows that the lack of older elephants in a population triggers the expression of aberrant behaviour and hyper-aggression in young males that, however, can be successfully reduced by re-introducing adult males [2,13]. Likewise, the introduction of adult domestic horses in same age - same sex groups of young appeared to decrease aggression rates and increase positive social interactions, compared to controls without similar introductions [14].

Beyond the mere presence or absence of adults, the adult-young ratio (i.e. the relative proportion of adults in a group) appears to be an important factor for social development, both in animals and in humans. Thus, this ratio plays an essential role in song acquisition in European starlings [15,16] and in human language development [17]. A high adult-child ratio in child-care centres is one of the strongest predictors of positive care-giving and high cognitive developmental rates of children [18,19]. Children are more responsive to their environment, have higher language acquisition rates and better global communication skills when adult-child ratios are high [20,17]. An anecdotal report of the effects of adult-young ratios on social behaviour is also given by Campbell monkeys, *Cercopithecus c. campbelli*: the removal of two adult females from a captive group led, among others, to the increase of aggression rates between young cage-mates [21].

However, no studies have systematically investigated the potential link between adult-young ratios and other aspects of social behaviour of young animals, such as aggression rates and social cohesion, especially in natural settings. Here, we observed

naturally-formed groups with various adult-young ratios and hypothesized that adult-young ratios would influence aggression rates and social cohesion of young Przewalski horses, *Equus f. przewalskii*. Young horses live in parental families (including one adult stallion, usually their father, two to five mares including their mother and their one- to three-year old offspring) until sexual maturity (two to three years) [22]. Pioneer studies showed that young domestic horses are sensitive to adult influences (e.g. mothers [23,24], unrelated adults [14]). Here, we show for the first time that adult-young ratios are directly correlated to the expression of aggression and to the social cohesion of young horses in their family group, aspects that affect the social skills of young horses.

Results

The 12 focal animals were one- and two-year-old Przewalski horses belonging to five families with adult-young ratios (AYR = - number of horses over three years old in the group / number of horses three years old and under) ranging from 0.67 to 1.33. Aggressive and positive interactions and spatial proximity to the nearest neighbour were recorded during direct observations. Spatial relationships were then assessed by calculating the proportion of time spent with each nearest neighbour and the corresponding inter-individual distances, to estimate affinities between individuals [25, see methods].

Aggression rates and spatial relationships varied significantly with adult-young ratios when the factor group size effect was kept constant (see methods). Adult-young ratios were negatively correlated with aggression rates (Kendall partial coefficient: $T = -0.54$, $p<0.02$, Fig. 1), which were up to four times higher in groups with the lowest proportions of adults (Na: mean number of aggressive interactions; $Na_{(AYR = 1.33)} = 3.25 \pm 1.65$; $Na_{(AYR = 0.67)} = 13.67 \pm 3.71$).

Adult-young ratios were also negatively correlated to time spent close to young nearest neighbours: the higher the proportion of young, the longer young remained close to their nearest neighbours, especially young neighbours to the detriment of adults (Fig. 2ab; Kendall partial coefficients: time spent at less than 0.5 horse body-length from nearest neighbour, $T = -0.44$, $p<0.05$; time spent with a nearest young neighbour, $T = -0.44$, $p<0.05$; time spent at more than 3.5 horse body-length from nearest neighbour, $T = 0.66$, $p<0.01$; time spent with a nearest adult neighbour, $T = 0.44$, $p<0.05$).

We therefore verified that the preferences/avoidances of young for partners were not merely proportional to the availability of partners in their group (see methods for calculations). Analyses revealed that the lower the adult-young ratio, the more young avoided some partners (Kendall partial coefficient: $T = -0.53$, $p<0.02$), especially adults: young had an adult as their nearest neighbour consistently less often than expected by chance (in all groups: mean number of young partners avoided $= 0.58 \pm 0.23$, mean number of adult partners avoided $= 2.42 \pm 0.26$; one-sample permutation test: $p = 0.002$).

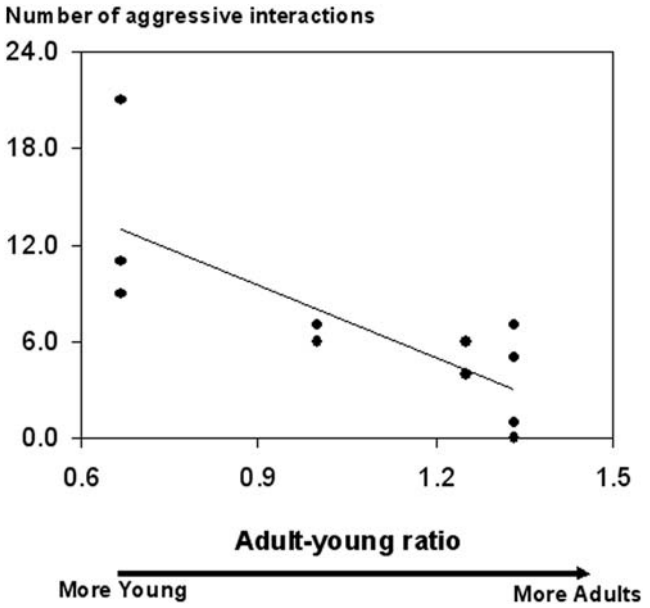

Figure 1. Aggression by young in relation to adult-young ratios in their family groups. *N*: number of aggressive interactions performed by young in 10 hours. Kendall partial coefficient correlation, $p<0.02$.
doi:10.1371/journal.pone.0004888.g001

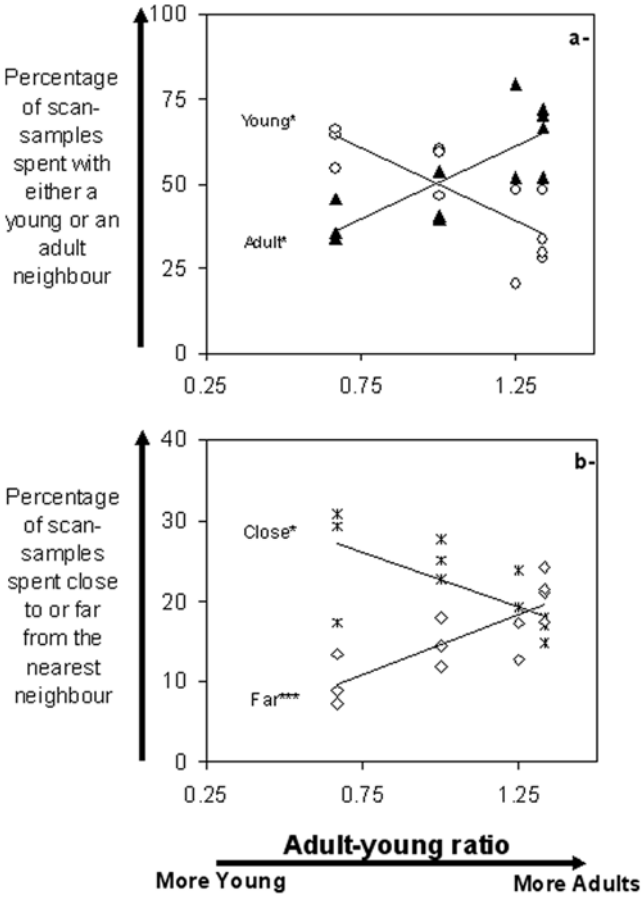

Figure 2. Spatial relationships of young Przewalski horses with their nearest neighbour in relation to adult-young ratios. a- Time spent with either a young neighbour or an adult neighbour, in relation to the adult-young ratio, b- Time spent close to or far from the nearest neighbour, in relation to the adult-young ratio. Time is expressed in percentage of scan-samples recorded in the field. Black triangles: adults; white circles: young; white squares: far from nearest neighbour (farther than 3.5 Horse Body-Length); stars: close to nearest neighbour (less than 0.5 Horse Body-Length). Categories ''close'' and ''far'' are not exclusive alternatives. Kendall partial coefficient correlation: * $p<0.05$, *** $p<0.01$.
doi:10.1371/journal.pone.0004888.g002

However, adult-young ratios significantly influenced neither spatial partner preference (i.e. number of preferred spatial partners, see methods), nor quantity of positive contacts, nor distribution in the other distance classes (Kendall partial coefficient: $p>0.05$ in all cases).

Discussion

This study clearly demonstrates how the ratio of adults to young in social groups of horses correlates with aggression rates and social cohesion. Thus, we showed that when, in a group, adult-young ratios were low, young horses were more aggressive, segregated more from adults and established tighter bonds with other young. This is, to our knowledge, the first study investigating the effects of adult-young ratios on aggression rates and social cohesion.

The adult-young ratios observed in this Przewalski horse population are similar to those observed in feral horse populations (e.g. from 0.50 to 1.30 [22,26]). The fact that aggression rates of young and their spatial relationships varied with this ratio means that developmental pathways experienced naturally by young can differ significantly in relation to group composition. These findings highlight the major role adults play in channelling aggressive behaviour (e.g. African elephants [6,13], cowbirds [11], domestic horses [14]), but they also suggest strongly that the influence of adults depends on their relative numbers. This therefore raises the important question of the consequences of early-stage variations of adult-young ratios on the long-term acquisition of social skills as well as on the functioning and the efficiency of groups. Only long-term experimental manipulations of adult-young ratios in groups could fill this gap in our understanding.

In addition, we found that young in groups with lower proportions of adults formed closer relationships and more selective bonds with peers than did young in groups with higher proportions of adults, who spent more time with an adult nearest neighbour, although it was farther away. Although the presence of adults sometimes seems to induce closer associations between young (e.g. cowbirds [11], domestic horses [14]), other studies [15,16], including this one, specify that associations between young could depend on the adult-young ratio: low proportions of adults in social groups induce more social segregation between young and adults than do high proportion of adults. These results are of interest for understanding developmental processes because social learning usually mirrors social preferences in groups [27]. Songbirds provide a good example of this process. Young starlings learn more from their preferred associates [28], and adult-young segregation, even in the presence of adults, induces young to neglect and to learn less songs from adult tutors [29,15]. The best adult-young ratio to induce song learning from adults appears to be 1:1 [15,16]. Lower attention paid by young to adults induces deficiencies in their central sensory area similar to those observed in socially-deprived animals, thus social segregation and physical separation from adults can have similar effects [30].

Interestingly, a decrease of selective attention appears spontaneously in children too: toddlers pay less attention to their mothers during visits by a same-age peer [31]. Adult-child ratios in child-care centres are known to affect the cognitive and language development of young through the quantity and quality of adult-child interactions [17]. When adults are proportionally fewer in relation to the number of children, caregivers tend to interact less with the children and to use more authoritarian and restrictive speech that does not stimulate language development and learning [19,32].

In horses, the exclusive relationship between foal-mare dyads induces foals to learn from their mothers since birth [23], but the strength of their mothers' influence decreases as the foals grow older [24]. However, one- and two-year-old horses are susceptible to the influence of unrelated adults [14]. Globally, these findings suggest that partners other than mothers could act as social models for older young, but that the proportion of young present in a group could regulate this influence by impairing either attention paid to adults or accessibility to adult partners [11,15]. In a sense, tighter bonds between young in groups with low proportions of adults could be a factor decreasing attention paid to adults and could probably reduce their influence as regulators of the behaviour of young, in particular their aggressive behaviour. However, at this point more research is needed to explain how adult partners, considered as social stimulations of the development of young, are shared by young members of a social group and how young horses establish their social preferences.

Furthermore, this study raises fundamental questions about the impact of adults on the development of young and opens a new line of research investigating the influence of various factors implied. Thus, adult-young ratios appear to be an important feature of social settings that must be taken into account as a potential modulator of social influence when evaluating developmental processes. Furthermore, this is true for child-adult ratios in classes, which is a concern of American [17] or European legislations, but not some countries such as France (Eurydice: http://eacea.ec.europa.eu/portal/page/portal/Eurydice/).

This insight therefore has practical implications as it highlights the importance of taking adult-young ratios and their effects on learning and social behaviour into account, both for management of animal groups and potentially child schooling.

Materials and Methods

Focal animals and housing conditions

The studied population of Przewalski horses (*Equus ferus przewalskii*) lives in a 380 ha enclosure of highland steppe at Le Villaret on the Causse Méjean (southern France). This population grew from 11 individuals brought from zoos in 1993 and 1994. Groups then formed naturally without human intervention until 2003, when there were 55 individuals. Observations were recorded during two periods (May and June 2004; April and May 2005) and focused on five families of seven to 12 horses with adult-young ratios similar to the ratios previously observed at the study site and in their natural environment [22,26]. We calculated adult-young ratios by dividing the number of horses that were over three years old in the group by the number of horses that were three years old and under, as Przewalski horses are adult when they are three years old [33]. Our focal animals were 12 juveniles from these five families: three one-year-old males, three one-year-old females, three two-year-old males and three two-year-old females (Table 1).

Table 1. Focal horses in their family groups.

Family number	Focal horse
Family 1	1f5, 1f6, 1m5 (N total = 12)
Family 2	1f7, 1m11 (N total = 9)
Family 3	1m6, 2f2, 2f3 (N total = 10)
Family 4	2f4, 2m4 (N total = 7)
Family 5	2m12, 2m7 (N total = 7)

Each horse was given an individual code indicating its age, sex and individual number. Ex: 1f5 is a one-year-old female, number five.
doi:10.1371/journal.pone.0004888.t001

Behavioural observations

We observed our subjects for two hours, twice a day, during five time-slots covering the day-light period: 0700–1000 hours, 1000–1300 hours, 1300–1530 hours, 1530–1800 hours and 1800–2100 hours. During each observation session, 10-minute scan-samples recorded the whole group, and each focal horse was observed continuously for 10-minute sampling sessions [34]. Each horse was observed for 10 hours in all. The two observers involved each year (M. B. & M. M. in 2004, M. B. & A. B.R. in 2005) recorded 25% of the observation sessions simultaneously to improve data reliability, which was controlled using Cohen's [35] kappa coefficient, that was $k = 0.95$.

Group scan-samples recorded the identity of, and distance to, nearest neighbour as spatial proximity is commonly used to estimate affinities between horses [25]. Distances to nearest neighbour were scored by classes of 0.5 Horse Body-Lengths (HBL) from 0.5 to 3.5 HBL and by a class (i.e. far) when distances were greater than 3.5 HBL. "Close" distances to the nearest neighbour corresponded to 0.5 HBL. "Far" distances to the nearest neighbour were scored for all distances exceeding 3.5 HBL from the nearest neighbour. Times spent in each distance class and near different neighbours were calculated in percentages of scan-samples, before analysis. Social interactions were recorded continuously during focal sampling and were expressed as number of occurrences for 10 hours. Social interactions were divided into two categories: (i) aggressive interactions, including head-threat, kick-threat, bite, kick and chase and (ii) positive contacts in the group, including approach, olfactory investigation, mutual grooming and head-body contact.

Statistical analyses

Preferential spatial partners were identified within family groups and based on spatial proximity to nearest neighbours. Spatial preferences were not necessarily reciprocal; for instance, although individual A is B's nearest spatial partner, A's nearest neighbour could be either B (reciprocity) or C, another individual closer to it than B (non-reciprocity). Individual A's preferential spatial partners were individuals that were the closest to A more frequently than expected by chance (partitioned chi-square goodness-of-fit test, Siegel & Castellan, 1988). Avoidance of spatial partners was calculated following the same method.

As group size varied among families, Kendall partial correlation coefficients (Kendall partial coefficient) analysed our data by keeping group size constant [36]. A one-sample permutation test compared the number of young and adult partners significantly avoided by the young in all groups. All tests were two-tailed, with a significance threshold of 0.05, and performed under StatXact 4.0.1 (Cytel Software Corporation). All means are given ±SE.

Acknowledgments

We are grateful to the Mava foundation and the Station Biologique de la Tour du Valat for logistic support and to Maïc Moulinot and Elodie Vigneron for their field and computing work. We also greatly thank Claudia Feh, Bernard Thierry, Marie-Annick Richard-Yris, Raphaël Clément and the two anonymous reviewers for their helpful comments as well as Dr Ann Cloarec for correcting English.

Author Contributions

Conceived and designed the experiments: MB MH. Performed the experiments: MB AdBdR. Analyzed the data: MB AdBdR. Contributed reagents/materials/analysis tools: MB AdBdR MH. Wrote the paper: MB AdBdR MH.

References

1. West MJ, King AP, White DJ (2003) The case for developmental ecology. Anim Behav 66: 617–622.
2. Bradshaw GA, Schore AN, Brown JL, Poole JH, Moss CJ (2005) Elephant breakdown. Nature 433: 807.
3. Thorallsdottir AG, Provenza FD, Balph DF (1990) Ability of lambs to learn novel food while observing or participating with social models. Appl Anim Behav Sci 25: 25–33.
4. Voelkl B, Schrauf C, Huber L (2006) Social contact influences the response of infant marmosets towards novel food. Anim Behav 72: 365–372.
5. Seyfarth RM, Cheney DL (1986) Vocal development in vervet monkeys. Anim Behav 34: 1640–1658.
6. McComb K, Moss C, Durant SM, Baker L, Sayialel S (2001) Matriarchs As Repositories of Social Knowledge in African Elephants. Science 292: 491–494.
7. West MJ, King AP, Freeberg TM (1997) Building a social agenda for the study of bird song. In: Snowdon CT, Hausberger M, eds. Social influences on vocal development. Cambridge: Cambridge University Press. pp 157–177.
8. White DJ, King AP, West MJ (2002) Facultative development of courtship and communication in juvenile male cowbirds (*Molothrus ater*). Behav Ecol 13: 487–496.
9. Kuhl PK (2003) Human speech and birdsong: communication and the social brain. Proc Natl Acad Sci USA 100(17): 9645–9646.
10. Pettit GS, Bates JE, Dodge KA, Meece DW (1999) The impact of after-school peer contact on early adolescent externalizing problems is moderated by parental monitoring, perceived neighborhood safety, and prior adjustment. Child Dev 70: 768–78.
11. White DJ, King AP, Cole A, West MJ (2002) Opening the social gateway: early vocal and social sensitivities in brown-headed cowbirds (*Molothrus ater*). Ethology 108: 23–37.
12. Hausberger M, Henry L, Cousillas H, Mathelier M, Bourjade M (2006) Social experience, vocal learning and social cognition in the European starling, *Sturnus vulgaris*. Acta Zool Sin 52(supplement): 618–621.
13. Slotow R, van Dyk G, Poole J, Page B, Klocke A (2000) Older bull elephants control young males. Nature 408: 425–426.
14. Bourjade M, Moulinot M, Henry S, Richard-Yris MA, Hausberger M (2008) Could adults be used to improve social skills of young horses, *Equus caballus*? Dev Psychobiol 50: 408–417.
15. Bertin A, Hausberger M, Henry L, Richard-Yris MA (2007) Adult and peer influences on starling song development. Dev Psychobiol 49: 362–374.
16. Bertin A, Hausberger M, Henry L, Richard-Yris MA (2008) Adult/young ratio influences song acquisition in a female European starling (*Sturnus vulgaris*). J Comp Psychol; In press.
17. Burchinal MR, Roberts JE, Riggins RJ, Zeisel SA, Neebe E, et al. (2000) Relating quality of center-based child care to early cognitive and language development longitudinally. Child Dev 71: 339–357.
18. NICHD Early Child Care Research Network (1996) Characteristics of Infant Child Care: Factors Contributing to Positive Caregiving. Early Childhood Research Quarterly 11: 269–306.
19. Howes C, Rubenstein J (1985) Determinants of toddlers' experiences in care: Age of entry and quality of setting. Child Care Quarterly 14: 140–151.
20. Burchinal MR, Campbell FA, Bryant DM, Wasik BA, Ramey CT (1997) Early intervention and mediating processes in cognitive performance of children of low-income African-American families. Child Dev 68: 935–954.
21. Lemasson A, Gautier JP, Hausberger M (2005) A brief note on the effects of the removal of individuals on social behaviour in a captive group of campbell's monkeys (*Cercopithecus campbelli campbelli*): a case study. Appl Anim Behav Sci 91: 289–296.
22. Boyd L, Keiper R (2005) Behavioural ecology of feral horses. In: Mills D, McDonnell S, eds. The domestic horse. The evolution, development and management of its behaviour. Cambridge: Cambridge University Press. pp 55–82.
23. Henry S, Hemery D, Richard M-A, Hausberger M (2005) Human-mare relationships and behaviour of foals toward humans. Appl Anim Behav Sci 93: 341–362.
24. Henry S, Briefer S, Richard-Yris M-A, Hausberger M (2007) Are 6-month-old foals sensitive to dam's influence? Dev Psychobiol 49: 514–521.
25. Feh C (2005) Relationships and communication in socially natural horse herds. In: Mills D, McDonnell S, eds. The domestic horse. The evolution, development and management of its behaviour. Cambridge: Cambridge University Press. pp 83–93.
26. Feist JD (1971) Behavior of feral horses in the Pryor Mountain wild horse range. PhD Thesis, University of Michigan. 130 p.
27. Coussi-Korbel S, Fragaszy DM (1995) On the relation between social dynamics and social learning. Anim Behav 50: 1441–1453.
28. Hausberger M, Richard MA, Henry L, Lepage L, Schmidt I (1995) Song sharing reflects the social organisation in a captive group of European starlings (*Sturnus vulgaris*). J Comp Psychol 109: 222–241.

29. Poirier C, Henry L, Mathelier M, Lumineau S, Cousillas H, Hausberger M (2004) Direct social contacts override auditory information in the song-learning process in starlings (*Sturnus vulgaris*). J Comp Psychol 118: 179–193.
30. Cousillas H, George I, Henry L, Richard JP, Hausberger M (2008) Linking social and vocal brains: Could social segregation prevent a proper development of a central auditory area in a female songbird? PLoS ONE 3(5): e2194. doi:10.1371/journal.pone.0002194.
31. Rubenstein J, Howes C (1976) The effects of peers on toddler interaction with mother and Toys. Child Dev 47: 597–605.
32. Mc Cartney C (1984) Effect of quality of day care environment on children's language development. Dev Psychobiol 20: 244–260.
33. Monfort SL, Arthur NP, Wildt DE (1994) Reproduction in the Przewalski's horse. In: Boyd L, Houpt KA, eds. Przewalski's horse, the history and biology of an endangered species. New York: State University of New York Press. pp 173–193.
34. Altmann J (1974) Observational study of behaviour: Sampling methods. Behaviour 49: 227–267.
35. Cohen J (1960) A coefficient of agreement for nominal scales. Educ Psychol Meas 20: 37–46.
36. Siegel S, Castellan NJ (1988) Nonparametric statistics for the behavioral sciences. Singapore: McGraw-Hill international. 399 p.