

Relationship of the Type of Social Organization to Scent-Marking and Mutual-Grooming Behaviour in Grevy's (*Equus Grevyi*) and Grant's Zebras (*Equus burchelli bohmi*)

Rikako KIMURA^{1, 2*}

¹Laboratory of Animal Management, Graduate School of Bioagricultural Sciences, Nagoya University, Nagoya and ²Equine Museum of Japan, 1-3 Negishidai, Naka-ku, Yokohama 231-0853, Japan

The social organization of three populations of 2 species of zebras in Kenya and its relationship to their communication behaviour were studied. Grant's zebras (Equus burchelli bohmi) (GTZ) inhabiting a dry savanna area had a harem-type social organization. Grevy's zebras (Equus grevyi) inhabiting a dry savanna area with many bushes, formed a territorial society (GYZ-1). Grevy's zebras (GYZ-2) inhabiting the same area as GTZ, created groups of a few to 20 males and females, bachelor groups and solitary males in the rainy season, and formed large groups of over 100 males and females in the dry season. The GTZ displayed three types of scent-marking, but GYZ-1 showed seven types, and GYZ-2 four types. In the GTZ the frequency of scent-marking with the urine of males on the urine of females (FUU) in the rainy season, and in the GYZ-1 the frequency of scent-marking with the faeces of males on his own faeces (MFF) during both seasons, were each significantly higher than other types of scent-marking in the respective groups. In the GYZ-2 male/female mixed groups, the frequency of FUU was significantly higher during the rainy season than during the dry season. The frequency of mutual grooming and mutual chin-resting in the GTZ was each significantly higher than that in the GYZ-1 or GYZ-2. Mutual chin-resting was occasionally observed in the GYZ-2. Neither mutual grooming nor mutual chin-resting was observed in the GYZ-1. These results suggest that the type and frequency of communication behaviour differs depending on the type of social organization in Equus species.

Key words: mutual-grooming, scent-marking, social type, zebra

J. Equine Sci.
Vol. 11, No. 4
pp. 91-98, 2000

Studies of the social organization and behaviour of various Equus species [2, 7, 12, 13, 15, 17-20, 22, 26, 28-35, 37-39] indicate that there are two basic types of social organization among Equus species. Several Equus species exhibit the harem-type of social organization, in which the horses form long-lasting, non-territorial family groups composed of one stallion and several mares with their foals. Other Equus species exhibit the territorial type of social organization, in which several estrous mares or mares with their foals stay in the territory of a stallion for a short period [21]. In Grevy's zebras, Ginsberg and his associate reported that the reproductive condition, i.e., whether a male

forms a harem or territorial group, determines the priority a female places on food and water [8, 9].

Regarding the communication behaviour in Equus species, Klingel [22] reported that in Grevy's zebras and wild asses that form a territorial society, scent-marking has visual and olfactory informational functions that show the male's boundaries or help to orienteer inside its territory by depositing its own dung piles along the boundary of its territory. In studies on the behaviours of other zebras and feral horses, it was proposed that the scent-marking behaviour of these animals that form a harem-type society serves to mask the reproductive information of the mares or to demonstrate the presence of the stallion, by scent-marking the urine or faeces of the mares with the urine of the stallion in the group [35, 36].

This article was submitted October 18, 2000 and was accepted November 14, 2000.

*2corresponding author.

Mutual grooming is considered to strengthen the bonds between individuals in the harem type society [4], decrease the rate of their heartbeat [6], and appease each of two individuals. This behaviour is observed between group members, between a mare and her foals, and among siblings in a group of feral horses. The frequency of mutual grooming changes with the season [15, 37, 38].

Although the scent-marking behaviour and mutual grooming behaviour are typical forms of communication behaviour involving the senses of smell, sight and touch, such behaviour has not been quantitatively compared among different *Equus* species. In this study the types and frequency of communication behaviour including scent-marking behaviour and mutual grooming behaviour, were compared among three zebra populations of two species with different types of social organization.

Methods

Animals

Grevy's zebras are the largest *Equus* species. The mean body weight of an adult male is approximately 431 kg, and that of an adult female is approximately ten percent less [16]. The female zebras give birth throughout the year, and the birth rate in August (Dry season) is slightly higher than those in other months [16]. A definite breeding season does not exist because copulation is observed in both the rainy and the dry season [16]. The pregnancy period is approximately 409 days [10]. Females are in estrous within 10 days after the previous birth and the heat lasts for 6–15 days [16]. If the female does not become pregnant again, the estrous cycle is repeated every 27 days [8].

Grevy's zebras generally form a territorial type of social organization. Some Grevy's zebras live in a semi-arid area where there are many bushes, whereas others live in a desert area. A male mates with estrous females that enter the territory. A female stays in the territory for 1–48 hr. Some females are monandrous and remain in the same territory, while others are polyandrous and emigrate to other territories to mate with other males.

The body weight of an adult male Grant's zebra is approximately 250 kg, and that of an adult female is approximately ten percent less [16]. The pregnancy period is approximately 1 year [10]. Females enter estrous a few days after the previous birth and the heat

lasts for 2–9 days. If the female does not become pregnant again, the estrous cycle is repeated every 17–24 days [16]. Although these zebras give birth throughout the year, most births are seen during the rainy season [16]. Their breeding season is considered to be in the rainy season, that is, March to May. They live in the savanna area and form harem-type groups. A family group consists of a stallion, several mares and their foals. The mares are basically monandrous and mate with a stallion in the same group.

Location of the study

This investigation was carried out in Samburu National Reserve of Samburu District and Buffalo Springs National Reserve of Isiolo District in Kenya. Samburu National Reserve is located in an arid area and there are many bushes. Buffalo Springs National Reserve is located on the east side of the Ewaso Ngiro River, and consists of a mosaic pattern of grassy areas and areas with bushes and rubble [1].

The present study included Grant's zebras and Grevy's zebras that inhabit two different areas. The Grant's zebras (GTZ) inhabit the grassy plains in the vicinity of the artificial pond located between the Chokaa Gate of Buffalo Springs National Reserve and the shrub area, which include plenty of rubble (2.5 km²). The Grevy's zebras that inhabit the area along the river between the West Gate and the Archer's Post Gate of Samburu National Reserve were designated as the GYZ-1 group. Approximately ten territorial groups were observed. Grevy's zebras that inhabit the grassy plains, with an area of approximately 20 km² near the artificial pond located on the west side of Chokaa Gate of Buffalo Springs National Reserve, were designated as the GYZ-2 group. These animals share the grassy plains with GTZ.

Sampling methods

The time and frequency of each communication behaviour (scent-marking behaviour, mutual grooming behaviour and mutual chin-resting behaviour) were obtained by the focal animal sampling method and the behaviour sampling method [25]. The animals were observed through a pair of field binoculars (8–20 × 24) at a distance of 5 to 30 m from the animals. Individual animals were identified by the specific pattern of stripes on the coat of each animal during the observation period in each season. Some of the GTZ, GYZ-1 and GYZ-2 zebras observed during the rainy season were the same individuals as those observed during the dry

season. Scent-marking forms of behaviour were defined as follows.

Scent-marking behaviour:

FFU: An animal (almost always male) sniffs the faeces of a female immediately after elimination. Sometimes the animal has a flehmen response after sniffing. The animal voids urine onto or next to the faeces.

FUU: An animal (almost always male) sniffs the urine of a female immediately after excretion. Sometimes the animal has a flehmen response after sniffing. The animal excretes urine onto or next to the spot of urine.

FUF: An animal (almost always male) sniffs the urine of a female immediately after it is voided. Sometimes the animal has a flehmen response after sniffing. The animal eliminates faeces onto or next to the spot of urine.

FFF: An animal (only male) sniffs the faeces of a female immediately after elimination. Sometimes the animal has a flehmen response after sniffing. The animal eliminates faeces onto or next to the faeces.

MFU: An animal (only male) sniffs the faeces of a male immediately after elimination. The animal voids urine onto or next to the faeces.

MFF: An animal (only male) sniffs the faeces of a male or faecal piles. The animal eliminates faeces onto or next to the faeces or faecal piles. After that, sometimes the animal sniffs his own faeces in the pile.

MUU: An animal (only male) sniffs the urine of a male immediately after it is voided. The animal voids urine onto or next to the spot of urine.

A series of a particular types of behaviour were recorded as one event (Fig. 1). The number and type of events in the scent-marking behaviour of each animal were recorded every day. The number of events in mutual grooming and mutual chin-resting behaviour of each animal was recorded every day.

The field observation was conducted during the daytime (7–8 hr/day) for 15 days each in August, 1998 (dry season; total observation time for 3 groups of zebras, 750 hr) and May, 1999 (rainy season; total observation time for 3 groups, 634 hr). Three staff members observed their own group of zebras for 15 days. The total number of animals observed during the dry and rainy seasons was: 70 GTZ zebras [17 males (9 in the dry season and 8 in the rainy season) and 53 females (28 in the dry season and 25 in the rainy season)], 133 GYZ-1 zebras [23 males (11 in the dry season and 12 in the rainy season) and 110 females (69 in the dry season and 41 in the rainy season)], and 188 GYZ-2 zebras [96 males (53 in the dry season and 43 in

the rainy season) and 92 females (44 in the dry season and 48 in the rainy season)].

Results

Social structure

The Grevy's zebras in the GYZ-1 group lived in territorial groups, each of which was composed of one male, 1–10 females, and young males, or in groups of non-territorial bachelor males. The GYZ-2 zebras formed different social organizations in the rainy and dry seasons. In the rainy season, several different groups of GYZ-2 were observed: (1) a social organization composed of approximately 20 males and females; (2) bachelor male groups; and (3) solitary males. In the dry season, they formed large male/female mixed groups, each of which was composed of over 100 individuals. The GTZ lived in harem groups of less than 10 animals, each of which was composed of one male and several females and foals. Other GTZ lived in bachelor male groups.

Communication behaviour

The frequency of a form of communication behaviour during the daytime (8 hr) in the GYZ-1 males, GYZ-1 females, GYZ-2 males, GYZ-2 females, GTZ males or GTZ females, was determined by dividing the number of times that the behaviour was observed in the animals in a group, by the total observation time for the animals in that group. The daily frequency of form of behaviour in an animal was calculated by converting it to frequency per one daytime (8 hr) per animal. The frequency of each form of communication behaviour per animal in each group is shown in Table 1.

Scent-marking behaviour

In the GYZ-1, all seven types of scent-marking behaviour were observed. The most frequently seen types of scent-marking in both the dry and rainy seasons was scent-marking with the faeces of the territorial males on their own faeces or on faecal piles in the territory (MFF) (Chi-square test: $\chi^2_6=22.9$, $p<0.001$) (Fig. 2).

In the GTZ animals which lived in harem-type groups, three types of scent-marking behaviour were confirmed. The most frequently seen type was scent-marking with the urine of males on the urine of females (FUU) (Chi-square test: $\chi^2_2=16.4$, $p<0.001$) (Fig. 2) in the same harem group in the rainy season (breeding

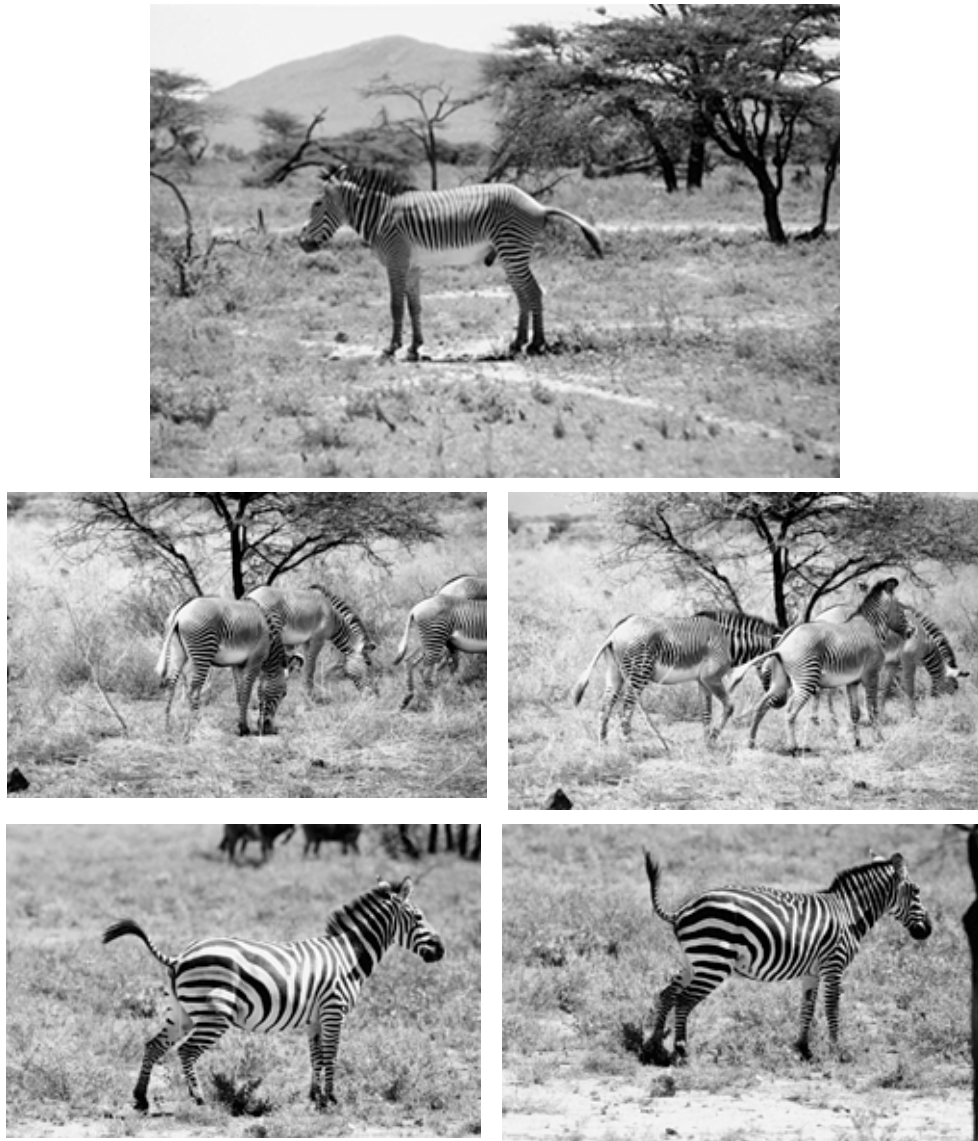


Fig. 1. Scent-marking behaviour: (upper) MFF by a male Grevy's zebra; (middle) FUU by a male Grevy's zebra; (lower) FUU by a male Grant's zebra (left, female; right, male). Photograph by Katsutoshi Ishiyama

season). In the GTZ group, scent-marking behaviour with the urine or the faeces of the male in a harem group on the faeces of females (FFU) (FFF) was the next most-frequently seen behaviour in both the rainy and dry seasons (Chi-square test: $\chi^2_1=0.07$, N.S.). In the GYZ-2, four types of scent-marking behaviour were confirmed. The most frequently-seen type in the GYZ-2 solitary males was marking the faecal piles of several males with faeces (MFF) (Chi-square test: $\chi^2_1=16.2$, $p<0.001$) (Fig. 2). In the GYZ-2 male/female mixed

group, the frequency of FUU during both seasons was the highest among the different types of scent-marking behaviour (Chi-square test: $\chi^2_2=8.2$, $p<0.02$) (Fig. 2).

A common scent-marking behaviour seen among all three zebra groups was FUU by males. Scent-marking with the urine of stallions on the faeces of males (MFU) was only seen in the GYZ-1 group in the dry season. Although the frequency of scent-marking behaviour of females was lower than that of males in all three zebra groups (Chi-square test: GYZ-1, $\chi^2_1=23.2$, $p<0.001$; GTZ,

Table 1. Mean frequency of communication behaviours during the daytime in male and female Grevy's zebras and Grant's zebras*

	FFU	FUU	FUF	FFF	MFU	MFF	MUU	MG	MCR
GYZ-1	(0.12)	0.21 (0.12)	0.42	(0.12)	(0.12)	0.63 (0.46)	(0.12)		
GYZ-1									
GYZ-2 G		0.72 (0.38)				0.07	0.14		0.07
GYZ-2 S						1.17			
GYZ-2			(0.22)						0.15
GTZ	0.59 (0.24)	2.38		0.40 (0.36)				0.20	1.78 (0.83)
GTZ	(0.04)	0.27 (0.04)						0.05 (0.07)	0.59 (0.56)

*The frequency of a particular behaviour in an animal in the indicated group during one day (8 hr), is shown. The frequency was obtained by counting the number of times the animals in a group performed a particular behaviour type of over the 15-day observation periods divided by the number of animals, and converted to per daytime (8 hr). (); dry season, FFU; marking female's faeces with urine, FUU; marking female's urine with urine, FUF; marking female's urine with faeces, FFF; marking female's faeces with faeces, MFU; marking male's faeces with urine, MFF; marking male's faeces with faeces, MUU; marking male's urine with urine, MG; mutual grooming, MCR; mutual chin-resting. G; males of mixed groups, S; solitary males.

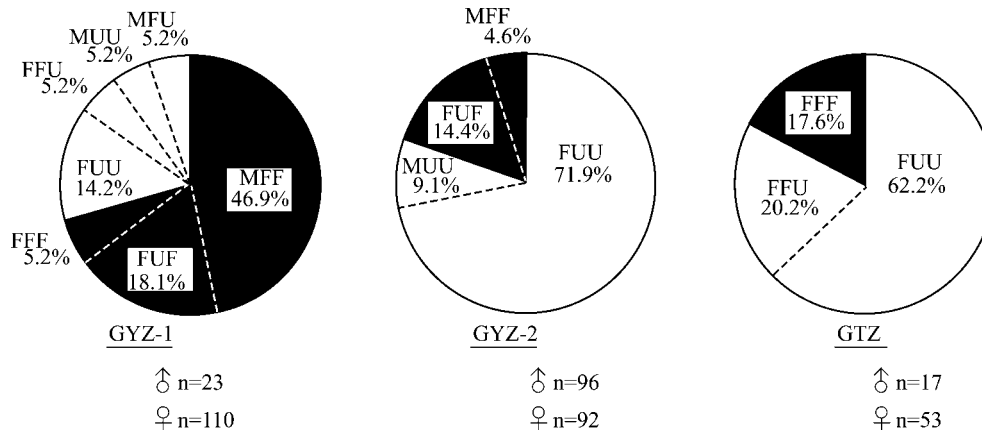


Fig. 2. Proportion of each type of scent-marking behaviour among the scent-marking types of behaviour of GYZ-1, GYZ-2, and GTZ in the rainy and dry seasons. The rate was calculated as follows: Number of events of a particular type of scent-marking behaviour in that population / Total number of events of all types of scent-marking behaviour in that population * 100.

$\chi^2_1=30.4$, $p<0.001$; GYZ-2, $\chi^2_1=19.0$, $p<0.001$), FFU and FUU by females in the GTZ, and FUF by female in the GYZ-2 were confirmed.

Mutual Grooming (MG) and Mutual Chin-Resting Behaviour (MCR)

MG was observed only in the GTZ zebras. Mutual chin-resting was observed in the GTZ group during the rainy and dry seasons, and in the GYZ-2 male/female

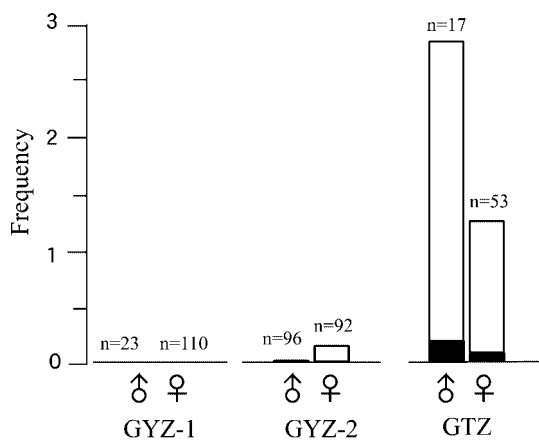


Fig. 3. Frequency of the mutual grooming and mutual chin-resting types of behaviour during a day in male and female GYZ-1, GYZ-2, and GTZ. The frequency was obtained by counting the number of times the animals in a group performed a particular behaviour over the 15-day observation period divided by the number of animals, and converted to per daytime (8 hr) in the rainy and dry seasons. mutual grooming, mutual chin-resting.

mixed groups during the rainy season. The frequency of MCR in the GTZ was higher than that in the GYZ-2 male/female mixed groups (Chi-square test: $\chi^2_1=51.30$, $p<0.001$) (Fig. 3). This behaviour was not seen in the GYZ-1 group (Fig. 3).

Discussion

In animals that form a harem-type society, a male basically mates with females inside the harem. Therefore, the purpose of scent-marking behaviour by a male zebra in a harem-type society is to mask the reproductive information of the females from males outside the harem [7, 27, 35]; thus scent-marking behaviour could be limited to three types (FUU, FFU and FFF) in the GTZ. In animals that form a territorial society, a male mates with an unspecified number of females which come and go in the territory. In the GYZ-1, seven different types of scent-marking behaviour (MFF, FUF, FFF, FUU, FFU, MUU and MFU) by a male against an unspecified number of females or males outside the group were observed. The purposes of scent-marking behaviour in male zebras in these groups are more diverse, and they could be

assumed to be the demonstration of boundaries [19, 20, 22], demonstration of the presence of a relationship with a female [3, 11, 14], removal [24] or masking of traces of invading males, masking the information of females [7, 28, 35], etc. In a population that forms a mixed society in between a harem-type and a territorial type society in accordance with the season (GYZ-2), at least four different types of scent-marking behaviour (FUU, MUU, FUF and MFF) were confirmed. These are in agreement with the theory of Krebs & Dawkins [23], in that if the sender of a signal and the recipient of a signal share a common interest, this should lead to cost-minimizing, muted signals, but if the sender of a signal and recipient of a signal do not share a common interest, this would lead to repetitive ritualized signals. This would also explain why Grant's zebras that form a harem-type society and do not share females with males outside the harem, express such behaviour.

Mutual grooming was observed only in the GTZ zebras. This behaviour has developed as a communication tool to maintain their family-type organization [4, 6] and has also the function of removing parasites [37]. The frequency of this behaviour in the GTZ that we studied seems to be less than the frequency of MG in zebras that inhabit the Ngorongoro National Reserve and more moist savanna areas [17]. The difference in frequency could be because of the difference of amounts of parasites in the two area [37]. In the present study, mutual chin-resting was more frequently observed than mutual grooming. Mutual chin-resting is performed by a pair of horses in a similar position as mutual grooming, but instead of scraping the coat with the incisors, the animal rests its chin on the back or hip of the other animal. This behaviour may be explained by the environment in which the GYZ-2 and GTZ live, which is a very dry area where there are fewer parasites. The mutual chin-resting behaviour may have been displaced by the mutual grooming behaviour in the Buffalo Springs National Reserve. The mutual chin-resting behaviour may have retained the function from the mutual grooming behaviour, and reduces the rate of the heartbeat of both animals [6], probably because of the physical contact with the other animal and by mutual appeasement. The mutual grooming behaviour was not observed in the GYZ-1 or GYZ-2 zebras. During the rainy season, however, the mutual chin-resting behaviour was occasionally observed in the GYZ-2 male/female mixed groups. The males and females in a GYZ-2 mixed group

stayed together for a longer time than the males in a bachelor group. In the GYZ-2 zebras, no mutual chin-resting behaviour was observed when the number of horses increased during the dry season.

Moehlman [30] reported that the frequency of mutual grooming behaviour in feral asses, in a mesic area that formed a harem-type society, was five times higher than that in feral asses in an arid area that formed a territorial society.

Acknowledgments

I thank Ms. Rieko Tanaka, Akiko Hasegawa, and Etsuko Momose for collecting two-thirds of all observation data in this study, and Mr. Richard Okubo and the staff of A & K for finding and chasing the target animal groups. I also thank Dr. Senichi Oda, Assistant Professor of Nagoya University, who advised me during the writing of this manuscript, and Dr. Shuko Osawa, Professor of Laboratory of Primates of Kyoto University, who gave me advice in planning the research. I also acknowledge the government of Kenya who gave me the opportunity to conduct this work, the staff of the offices of the Buffalo Springs and Samburu National Reserves who assisted me in conducting the work efficiently, and KWS who supported my work in Kenya.

References

1. Barkham, J.P. and Rainy, M.E. 1976. The vegetation of the Samburu-Isiolo Game Reserve. *East Afric. Wildlife J.* **14**: 297–329.
2. Berger, J. 1977. Organizational systems and dominance in feral horses in the Grand Canyon. *Behav. Ecol. Sociobiol.* **2**: 131–146.
3. Broterton, P.N.M. and Manser, M.B. 1997. Female dispersion and the evolution of monogamy in the dik-dik. *Anim. Behav.* **54**: 1413–1424.
4. Crowell-Davis, S.L., Houpt, K.A., and Carini, C.M. 1986. Mutual grooming and nearest-neighbor relationships among foals of *Equus caballus*. *Appl. Anim. Behav. Sci.* **15**: 113–123.
5. Ehrman, L. and Parsons, P.A. 1981. Behavior genetics and evolution. McGraw-Hill, New York.
6. Feh, C. and De Mazieres, J. 1993. Grooming at a preferred site reduces heart rate in horses. *Anim. Behav.* **46**: 1191–1194.
7. Feist, J.D. and McCullough, D.R. 1976. Behavior patterns and communication in feral horses. *Z. Tierpsychol.* **41**: 337–371.
8. Ginsberg, J.R. 1989. The ecology of female behaviour and male mating success in the Grevy's zebra. *Symp. Zool. Soc. Lond.* **61**: 89–110.
9. Ginsberg, J.R. and Rubenstein, D.I. 1990. Sperm competition and variation in zebra mating behavior. *Behav. Ecol. Sociobiol.* **26**: 427–434.
10. Grzimek, B. 1990. Grzimek's Encyclopedia of Mammals (Ed. Parker, S.P.) 4, McGraw-Hill, United States.
11. Hendrichs, H. 1975. Changes in a population of dikdik *Madoqua (Rynchotragus) kirkii* (Günther 1880). *Z. Tierpsychol.* **38**: 55–69.
12. Kaseda, Y. 1981. The structure of the groups of Misaki horse in Toi Cape. *Japanese Journal of Zootechnical Science* **52**: 227–235.
13. Keiper, R.R. 1976. Social organization of feral ponies. *Proceeding of the Pennsylvania Academy of Science* **50**: 69–70.
14. Kimura, R. 1995. An analysis of the sniffing, scent-marking behaviour and odorous fecal substances in Somali Wild Ass (in Japanese). *Bulletin of Equine Museum of Japan* **8**: 1–15.
15. Kimura, R. 1998. Mutual grooming and preferred associate relationships in a band of free-ranging horses. *Appl. Anim. Behav. Sci.* **59**: 265–276.
16. King, J.M. 1965. A field guide to the reproduction of the Grant's zebra and Grevy's zebra. *East Afric. Wildlife J.* **3**: 99–117.
17. Klingel, H. 1967. Soziale organisation und verhalten freibender steppenzebras (*Equus quagga*). *Z. Tierpsychol.* **24**: 580–624.
18. Klingel, H. 1968. Soziale organisation und verhaltensweisen von Hartmann und Bergzebras (*Equus zebra hartmannae* und *E.z.zebra*). *Z. Tierpsychol.* **25**: 76–88.
19. Klingel, H. 1972. Project 496. Somali wild ass: Status survey in the Danakil region. *World Wildlife Yearbook 1971–1972*: 75–81.
20. Klingel, H. 1974. Social organization and verhalten des Grevy-Zebras (*Equus grevyi*) *Z. Tierpsychol.* **36**: 37–70.
21. Klingel, H. 1975. Social organization and reproduction in Equids. *J. Reprod. Fertil. Suppl.* **23**: 7–11.
22. Klingel, H. 1977. Observations on social organization and behaviour of African and Asiatic Wild Asses. *Z. Tierpsychol.* **44**: 323–331.
23. Krebs, J.R. and Dawkins, R. 1984. Animal signals: mind-reading and manipulation. pp. 380–402. *In: Behavioural Ecology.* (Krebs, J.R. and Davis, N.B. eds.), Blackwell Scientific Publications, Oxford.

24. Leuthold, W. 1977. African Ungulates: a Comparative Review of Their Ethology and Behavioral Ecology. Springer-Verlag, Berlin.
25. Martin, P. and Bateson, P. 1986. Measuring Behaviour. Cambridge University Press, New York.
26. McCort, W.D. 1980. The Feral Asses (*Equus asinus*) of Ossabaw Island, GA. PhD thesis, Pennsylvania State University, University Park.
27. Miller, R. and Denniston, R.H. 1979. Interband dominance in feral horses. *Z. Tierpsychol.* **51**: 41–47.
28. Moehlman, P.D. 1979. Behavior and ecology of feral asses (*Equus asinus*). National Geographic Society Research Reports 1970: 405–411.
29. Moehlman, P.D. 1998a. Behavioral patterns and communication in feral asses (*Equus africanus*). *Appl. Anim. Behav. Sci.* **60**: 125–169.
30. Moehlman, P.D. 1998b. Feral asses (*Equus africanus*): intraspecific variation in social organization in arid and mesic habitats. *Appl. Anim. Behav. Sci.* **60**: 171–195.
31. Rubenstein, D.I. 1981. Behavioural ecology of island feral horses. *Equine Vet. J.* **13**: 27–34.
32. Rubenstein, D.I. 1986. Ecology and sociality in horses and zebras. pp. 282–302. *In: Ecological Aspects of Social Evolution.* (Rubenstein, D.I. and Warnham, R.W. eds.) Princeton University Press, Princeton NJ.
33. Salter, R.E. and Hudson, R.J. 1982. Social organization of feral horses in western Canada. *Appl. Anim. Ethology* **8**: 207–223.
34. Stahlbaum, C.C. and Houpt, K.A. 1989. The role of the flehmen response in the behavioral repertoire of the stallion. *Physiol. Behav.* **45**: 1207–1214.
35. Trumler, E. 1958. Beobachtungen an den Bohmzebras des George-von-opel-friegeheges fur Tierforschung: 1. Das Paarungsverhalten. *Saugetierkundliche Mitteilungen* **6**: 1–48.
36. Turner, J.W., Perkins, A., and Kirkpatrick, J.F. 1981. Elimination marking behavior in feral horses. *Can. J. Zool.* **59**: 1561–1566.
37. Tyler, S.J. 1972. The behavior and social organization of the New Foret ponies. *Anim. Behav. Monogr.* **5**: 85–196.
38. Wells, S.M. and von Goldschmidt-Rothschild, B. 1979. Social behaviour and relationships in a herd of Camargue horses. *Z. Tierpsychol.* **49**: 363–380.
39. Welsh, D.A. 1975. Population, behavioural, and grazing ecology of the horses of Sable Island, Nova Scotia. PhD thesis, Dalhousie University.