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Social Ecology of Horses

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Abstract

Horses (*Equidae*) are believed to formidably demonstrate the links between ecology and social organization. Their social cognitive abilities enable them to succeed in many different environments, including those provided for them by humans, or the ones domestic horses encounter when escaping from their human care takers. Living in groups takes different shapes in equids. Their aggregation and group cohesion can be explained by Hamilton's selfish herd theory. However, when and which group to join appears to be a conscious individual decision depending on predatory pressure, intra group harassment and resource availability. The latest research concerning the social knowledge horses display in eavesdropping experiments affirm the need for an extension of pure genetic herd concepts in horses for a cognitive component. Horses obviously realize the social composition of their group and determine their own position in it. The horses' exceedingly flexible social behavior eagerly demands for explanations about the cognitive mechanisms which allow horses to determine their individual decisions.

"Ecology conditions like those that favor the evolution of open behavioural programs sometimes also favor the evolution of the beginnings of consciousness, by favoring conscious choice. Or in other words, consciousness originates with the choice that are left open by open behavioural programs" (Popper, 1977).

1 Introduction

Horses (*Equidae*) are believed to formidably demonstrate the links between ecology and social organization (Berger 1977, Moehlmann 2002). Their social cognitive abilities enable them to succeed in many different environments, including those provided for them by humans, or the ones domestic horses en-

counter when escaping from their human care takers. Since horses show a strong tendency to gather in groups, it seems to be reasonable to apply Hamilton's selfish herd theory (1971) to herd aggregation and group cohesion in equids. Hamilton (1971) introduced the case of a novel mutant which increases its reproductive strategy by taking cover between its herd companions. Finally, the novel behaviour will spread throughout the whole population and initiate herd aggregation, which results in a better protection from predation for the herd members. This theory led to the assumption that simple selfish movement rules would decrease predation risk when the predator attacks from outside the flock perimeter (Viscido et al. 2001). And in fact Viscido et al. (2001) found that regardless of the predator's size and speed predation risk always decreases as long as the individuals take their mates into account. They concluded that the selfish avoidance of danger can lead to aggregation. However, Hamilton's (1971) movement rules are neglected to produce true aggregations, because the required complex individual behavior would be impossible for most animals to follow. Viscido et al. (2002) called this phenomenon the "dilemma of the selfish herd". In their opinion the animal's ability to detect its neighbors is an important factor in the dynamics of group formation. Not only the nearest neighbors but also the behaviour of distant neighbors mediates information in case of predation. Reluga and Viscido (2005) suggested that predation-based selection can even increase the influence of distant neighbors relative to near neighbors.

Another critical approach to the nearest neighbor strategy, proposed by Hamilton's selfish herd model, was written by James (2004). He introduced the concept of a "limited domain of danger", which represents either a limited detection range or a limited attack range of predators. An analysis of individual movement rules showed that animals escape from danger best, when they use a time minimization stra-

tegy rather than a nearest neighbor strategy.

Because of the horses' strong tendency to gather in groups, I agree that their basic aggregation and group cohesion can be explained by Hamilton's selfish herd theory (1971). However, the critical voices, which express criticism concerning the consideration of conscious neighbor detection should be considered, as well. When and which group to join appears to be a conscious individual decision depending on predatory pressure, intra group harassment and resource availability. For greater foraging efficiency, horses have to decide when to spread out, at a cost of greater predation risk (Janson 1990).

The social lives of equid herds can be compared to the fission-fusion model (Dyer 2000) in apes' social systems to some extent. Apes (Dyer 2000), elephants (Moss and Poole 1983) and dolphins (Connor et al. 2000) frequently depart and reunite again. However, most equids' social groups are much more stable, even though stallions change their reproductive strategy and therefore their social affiliation several times throughout their lives. Nevertheless mares tend to stay with the group they once joined after they departed from their natal group in their first estrus. Depending on predatory pressure and resource availability they sometimes change their affiliation to a certain social group even later in life. Though these capabilities are probably best known from feral horses (*Equus ferus caballus*) they have to be discussed in the context of the whole equid family.

Living in groups takes different shapes in equids. For species, which live in wide grasslands, such as the Serengeti Plain of Tanzania or the valleys of Hustai National Park in Mongolia (King 2005), food and water resources are sufficient enough to allow females to feed together and to thus form stable groups, which consist of one or more mares, their offspring and usually one, but occasionally up to five males (Tyler 1972, Berger 1977, Moehlmann 2002). Surplus stallions gather in separate bachelor groups that differ in size from 2 to approximately 17 horses (Berger 1977). Such a system is referred to as "harem", "family," or "band." Many bands form a structured social unit, called "herd," which shows the same migration patterns within a common home range (Miller 1979). Berger (1977) observed a herd of more than 210 feral horses grazing, clustered in groups. Harem groups are common in Plains and Mountain zebra (*Equus burchelli* and *E. zebra*), Przewalski's horses (*E. ferus przewalskii*), and feral horses (*E. ferus caballus*) and provide a relatively safe environment, as stable groups and the presence of a stallion help to fend off predators, such as wolves, lions, and hyenas.

Mature females of a band often remain together throughout their whole lives, while stallions may change their reproductive strategy several times, depending on their age and fighting ability and the number of competitors they have to contend with (Feh-

1999). Foals born into a group stay with it for one to five years before they disperse (Moehlmann 2002). Young females usually leave during their first estrus and join other families (Berger 1986). Young males tend to stay for several more years before they depart to find bachelor groups (Moehlmann 2002) or found a harem of their own. However, Klingel (1972) hypothesized that in the absence of playmates male offspring disperses earlier from their natal group. This "playmate hypothesis" is still under discussion. Berger (1986) could not find any correlation between dispersal age and number of peers in the feral horses of the "Great Basin", Nevada, Utah, Oregon, whereas Rutberg and Keiper (1993) could prove a strong correlation for male offspring dispersal age and the presence of playmates in Assateague Island ponies, Maryland. On average male offspring dispersed earlier than female offspring on Assateague Island.

When food biomass levels drop below 40 g/m² during periods of drought, normally stable groups of plains zebras may become unstable (Ginsberg 1988). This suggests that the stability of group and group size in equids is bound to the distribution and availability of resources. Especially in dry environments, such as the Danakil Desert of Ethiopia and Eritrea, the scattered supply of food and limited water usually does not permit females to forage close to one another and to form consistent groups. Therefore, males establish separate territories near a critical source of water or food. They then control mating with all females, which, sometimes accompanied by their offspring, come onto the territory to drink or feed (Moehlmann 2002). African wild asses (*E. africanus*), feral asses (*E. asinus*), Grevy's zebra (*E. grevyi*) and Asiatic wild asses (*E. hemionus*) organize themselves without permanent bonds between adults although sometimes they form temporary groups. Stallions can dominate their territories for years. They may tolerate other males in this area but monopolize mating.

Controlling access to water is critical. Lactating females need to drink at least once a day, and so they will stay as close to a pond or stream as possible. A female comes into estrus a week or two after giving birth and, if she is not fertilized then, again about a month later. Thus, the territorial male has several chances to father a new foal. The females, in turn, do not only gain access to water but may also benefit from reduced harassment from bachelor males and better protection from predators (Klingel 1977, Moehlmann 2002).

2 Ecology and social organization of feral horses

According to genetic data, horses, *E. caballus*, were domesticated repeatedly from several distinct populations of wild horses (Jansen et al. 2002). Today, all domestic and feral horses are organized in social groups. For a full understanding of the evolutionary

roots of their social behavior, a comparison with their wild ancestors would be of immense value. Unfortunately, Przewalski's horses, the last representatives of wild horses, are now declared to be extinct in their native habitats (Klimov and Orlov 1982). Those that still exist are descendants of 11 breeding animals, which themselves are descendants of 39 horses caught in the field and brought into European zoos between 1899 and 1902, plus one mare captured in Mongolia as a foal in 1947 (Ryder and Wedemeyer 1982). Almost nothing is known on their behavior in native habitats. Today they are kept in zoos (Kolter and Zimmermann 1988), in semi-wild reserves (Feh 1988), or reintroduced into the wild, for instance in the Hustai National Park, Mongolia (King 2005), where they form stable harem-type groups. It remains unclear, however, whether inbreeding has affected the behavior of Przewalski's horses and whether behavioral characteristics found in domestic and feral horses but not in Przewalski's horses, arose as a result of genetic drift, adaptation, or domestication (Berger 1986).

More insight in the "natural" behavior and social organization of domestic horses comes from the study of free ranging populations of feral horses. Ever since horses have been domesticated 2,500 - 5,000 years ago (Clutton-Brock 1981) they have escaped from their caretakers and organized themselves in free ranging groups. The process of feralization can be considered as successful if the escapees form stable populations, fare well, and reproduce. Stable populations of feral horses exist on islands of the North American Atlantic coast (Welsh 1975, Keiper 1979, Rubenstein 1981), in subhumid and arid plains of continental Australia (McKnight, 1976), deserts and mountains of western North America (Salter and Hudson 1982, Miller and Denniston 1979, Berger 1977), and the North Island of New Zealand (Cameron et al. 2003). Semi-wild populations are still managed in England's New Forest (Tyler 1972, Pollock 1980) and Exmoor preserves (Gates 1979), as well as in the Camargue Delta in France (Duncan 1980, v. Goldschmidt and Tschanz 1978, Feh 1999).

Feral horses form harem-type social organizations, usually consisting of one, in some cases up to five stallions, in which usually only the alpha and the beta stallion reproduce (Linklater et al. 1999, Feh 1999), and several mares and their offspring, which stay in the harem until maturity. Until now, the existence of single male bands and multiple male bands has not been sufficiently explained (Linklater and Cameron 2000, Feh 2001). The latter tend to be larger in group size and are consistently more stable than single male bands (Miller 1979). Female offspring eventually disperses to other harems, whereas male offspring form bachelor groups. Stallions usually change between different reproductive strategy, such as holding a harem, joining a bachelor group, or occasional sneak

mating, several times throughout their lives (Miller 1979, Feh 1999). Migrating females may join other bands or bachelor stallions (Berger 1986).

3 Environmental influences on feral horses group size

Along with primates, group-living ungulates are believed to show the best correlation between body size, ecology and social organization. In general, species that exploit open environments tend to be larger in size and more gregarious than those who live in limited habitats abundantly covered with vegetation. Body size is affected by food distribution and foraging locations, and at the same time has consequences on anti-predatory behavior and spatial distribution patterns (Eisenberg 1981, Geist 1978).

According to Waring (1979), the social organization of horses is strongly affected by the distribution of resources and individual distribution in space. Groups tend to be larger size in open environments than in bordered habitats, especially when resources are abundant. However, environmental stress such as severe weather conditions in winter as well as food limitation during dry seasons causes bands to split into smaller groups (Miller 1979), which then usually roam on vast, overlapping areas (Salter 1979). In contrast, in island habitats with limited dispersal, high frequencies of interactions, and evenly distributed resources, feral horse herds have been observed to live in non-overlapping home ranges (Zervanos and Keiper 1979) or to become territorial and repel intruding horses (Rubenstein 1978).

Parasites also appear to have a strong influence on group size at least in Camargue horses, for which Duncan & Vigne (1979) found a positive correlation between group size and the rate of attack by blood sucking flies. The per capita rate of bites was lower when horses gathered in large groups than in small ones.

Feral horses are challenged by only few effective predators, and reports on predation by wolves, lions and bears are anecdotal (Berger 1986). Humans, however, have a strong impact on group size and stability. The increase of the population size of feral horses in North America requires regulation by removal or translocation (U. S. Bureau of Land Management 2006). Such disruptions have a severe influence on the behavioral stability and the group size of herds as well as the well being of the horses. For example, Tyler (1972) reports that group size in New Forest ponies, in which nearly all the colts and fillies are removed in autumn or winter remained small. On Sable Island, a chain of sand dunes in the North Atlantic Ocean, a new inexperienced male moved the herd into regions with poor shelter and poor food quality after the loss of a herd stallion in winter (Welsh 1975).

4 The ecology of relationships in horses

Groups of horses are structured by dominance hierarchies, however, the exact meaning and nature of such hierarchies are discussed (Berger 1977, Ellard 1989, Houpt et al. 1978, Houpt and Wolski 1980, v. Goldschmidt-Rothschild and Tschanz 1977, Heitor et al. 2006). Dominance relationships among domestic horses have been commonly investigated by paired feeding tests, an interaction contest over the limited resource "food". However, Ellard (1989) mentioned that the results of such a test with draft-horse mares did not match her observations of the dominance hierarchy of the same horses in field. In recent studies, dominance relationships have been estimated by approach-retreat interactions and the direction of threats and submissive gestures (McDonnell and Haviland 1995, McDonnell 2003, Heitor et al. 2006), interactions that are thought to be correlated with the individual resource holding potential power (RHP) (Pusey and Packer 2003). In dyadic encounters, RHP is often a reliable predictor of the rank of interacting individuals. With increasing group size, it becomes less and less probable that dominance hierarchies are linear due to differences in RHP (Mesterton-Gibbons and Dugatkin 1995). Instead, the RHPs of animals for different resources are likely to overlap, as the value of different resources may vary between individuals and with time and situation. A hungrier animal, for example, would tolerate greater costs and thus fight longer and harder for food (e.g. Parker 1984, Houston and MacNamara 1988). In addition, dominance rank of horses appears to be correlated with age and the length of time the individual has resided in the group (Keiper and Sambras 1985, Linklater et al. 1999), both traits, which are uncorrelated with RHP (Pusey and Packer 2003). For an alternative concept of dominance relationships in horses, which matches non-linearity due to overlapping RHPs, Goldschmidt-v.Rothschild & Tschanz (1978) proposed to divide social groups into three dominance groups. All horses classified as members of one level (A, B or C) interact with each other and may change their social position within their respective group, depending on the situation, but horses of level A generally are dominant over those of levels B and C, and horses of level B are dominant over those of level C, regardless of the context.

Social status has also been discussed to be inherited. Houpt & Wolski (1980) investigated the social ranks which the offspring of ten thoroughbred mares receive in their own age groups after weaning. The foals of high-ranking mares tended to obtain similar ranks as their mothers, while foals of mares of middle and low dominance rank were not consistently found in the same rank position. In addition, Feh (1999) reported that the sons of low-ranking and high-ranking mares in Camargue horses, obtained similar ranks as their mothers throughout their reproductive period.

The proximate mechanisms leading to the heritability of social status are unclear. Individuals may learn by observing others as well as from their first few encounters with opponents (Huntingford and Turner 1987, Clutton-Brock and Parker 1995).

The occurrence of successful sneak mating (Feh 1999, Linklater and Cameroon 2000) relativizes the importance of RHP and dominance relationships for the reproductive success of male horses. Nevertheless, long term paternity data show that dominant stallions, which hold single stallion bands, have a higher reproductive success than stallions pursuing other mating strategies. In multi-male bands, the dominant stallion can sire the largest percentage of foals, but up to one third of matings can be ascribed to the beta stallion (Feh 1999, Linklater and Cameroon 2000). "Sneak mating" has had the lowest success (Feh 1999, Linklater and Cameroon 2000).

When separated from their herd companions, horses have a strong tendency to return to their social unit (e.g. Tyler 1972). Miller (1979) reports that male horses from bachelor groups or from other bands did not attempt to gain female horses that coincidentally were separated from their group. In contrast, wandering females are commonly accepted by band leading- or bachelor stallions (Berger 1986), but it is unknown how stallions realize that a mare is willing to be accompanied or integrated into a new group.

5 Cooperation and alliances

Hierarchies in horse herds are complicated by the formation of alliances and cooperation among individuals. In addition to single-male bands, multiple-male bands exist (Miller 1979, Berger 1986, Feh 1999, Linklater et al. 1999), which tend to be larger in group size and to be consistently more stable (Miller 1979). Whether this is due to the existence of alliances among stallions has recently been discussed (Feh 1999, Linklater et al. 1999, Feh 2001). In chimpanzees, alliances seem to destabilize dominance hierarchies but induce a state of mutual interdependence among individuals in lead to a greater access to resources (De Waal 1982, Nishida 1983). In multi-stallion bands of horses, the partners of dominant stallions are subordinate in rank. While the beta stallion has a higher reproductive success than subordinate stallions relying on "sneak mating," the dominant stallions of such bands sire fewer foals than dominant stallions from single-stallion bands. Stallions which join multi-stallion bands additional to the alpha and the beta stallion have been reported not to reproduce (Feh 1999, Linklater and Cameroon 2000). The advantage for the dominant stallions comes from the higher success of multi stallion bands to fend off rivals and to avoid sneak matings (Linklater and Cameroon 2000) and foal mortality appears to be lower in multi stallion than in single stallion bands (Duncan 1992,

Feh 1999). However, for Feh (1999) and Duncans (1992) data foal survival could still be linked with the foaling rate of the respective groups. In this respect, it would be worth reconsidering their data, since Linklater et al. (1999) can not support this hypothesis. Linklater et al. (1999) found that foaling rate, as well as offspring mortality, negatively correlates with the aggression rate stallions display towards their mares. In their data aggression rate is higher in multi stallion groups than in single stallion groups, which causes lower fecundity and a higher group travel rate in the mares. The latter directly correlates with offspring survival. However, Linklater et al.'s (1999) hypotheses are contradicted by Millers (1979) suggestions that multiple male groups are consistently more stable than single male bands.

Whether mares form alliances against stallions or other mares has as yet not been proved, though mares play a much larger part in the social lives of horse herds than stallions do. Goldschmidt von Rothschild and Tschanz (1978) suggest additional alliances among members of rank groups A, B and C. The occurrence of mutual grooming between stallions and mares was not correlated to their mating activities and independent of their individual ranks. Explanations of the patterns of social interactions and sexual affiliations are as yet unclear.

Another behavioral pattern that might fit into the category "cooperation and alliances" is "interference" (McDonnell and Haviland 1995, McDonnell 2003). In interferences, stallions move in between pairs of fighting stallions and thus disrupt their combat. This behavior has been observed in horses, Przewalski's horses (Keiper 1988), zebras (Schilder 1990) and Asiatic wild asses (Bannikov 1971).

6 Eavesdropping and Communicative Networks

In order to understand complex behavioral patterns, such as cooperation and alliances, it is necessary to analyze social interactions on the level of the signals individuals receive from their companions. Of particular interest is the behavior of uninvolved bystanders after eavesdropping on dyadic encounters among group members. It has recently been investigated what animals know about themselves and their social environment in fish, birds, and bats (McGregor 1993, Oliveira et al. 1998, Naguib et al. 1999, Dugatkin 2001, McGregor and Dablesteen 1996, Paz-y Miño 2004). For example, in Siamese fighting fish, bystanders were less aggressive towards the fish who won a previous interaction observed by the bystander than towards the fish who lost (Oliveira et al. 1998). Horses appear to similarly observe their social environment and to utilize information they draw from monitoring interactions among others. This is suggested by the fact that severe fighting is very rare, especially in well-settled harems (Berger 1986), as well

as in cases in which stallions did not attempt to gain female horses that coincidentally were separated from their group Miller (1979).

It was recently shown that bystander horses adjust their response to an experimenter according to their own dominance relationship with the horse whose reaction to the experimenter they had observed before. In an experiment that used the "round-pen" technique of "horse-whisperers" (Rivera et al. 2002, Sighieri 2003, Miller and Lamb 2005, Krüger 2007), bystander horses immediately followed the experimenter after previously watching a dominant horse doing so but did not follow after observing a subordinate horse or a horse from another social group doing so (Krüger and Heinze subm.). The results of this study suggest social reasoning in inter-specific dominance relationships and for the first time document observational learning in horses.

7 Conclusion

The latest research concerning the social knowledge horses display in eavesdropping experiments affirm the need for an extension of pure genetic herd concepts in horses for a cognitive component. Horses obviously realize the social composition of their group. They even are able to determine their own position in it. The horses' exceedingly flexible social behavior eagerly demands for explanations about the cognitive mechanisms which allow horses to determine their individual decisions. As Nicol (2002) already claimed, there is an urgent need for specific research in horses' cognitive abilities. Aside from basic cognitive research, especially, the assumption for the existence of alliances in horses (Feh 1999) needs to be evaluated more closely.

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References:

- Bannikov A G (1971) The Asiatic Wild Ass: neglected relative of the horse. *Animalia* 13: 580-585
- Berger J (1977) Organizational systems and dominance in feral horses in the Grand Canyon *Behav Ecol Sociobiol* 2:131-146
- Berger J (1986) *Wild horses of the great basin*. University of Chicago Press, Chicago and London
- Clutton-Brock J (1981) *Domesticated animals, from early times*. London: British Museum of Natural History.

- Clutton-Brock J, Parker GA (1995) Sexual coercion in animal societies. *Anim Behav* 49: 1345-1365
- Connor RC, Wells RS, Mann J, Read AJ (2000) The bottlenose dolphin: social relationships in a fission-fusion society. In: J Mann, R C Connor, PL Tyack and H Whitehead (eds) *Cetacean Societies: Field Studies of Dolphins and Whales*. pp 91-126 University of Chicago Press, Chicago
- De Waal F (1982) *Chimpanzee politics: power and sex among apes*. Harper and Row, New York
- Dugatkin LA (2001) Bystander effects and the structure of dominance hierarchies, *Behavioral Ecology*, vol.12, 3:348-352
- Duncan P (1980) Time-budgets of Camarque horses, 2: Time-budget of adult horses and weaned subadults. *Behaviour* 72:26-49
- Duncan P (1992) *Horses and Grasses*. Springer Verlag, New York
- Duncan P, Vigne N (1979) The effects of group size in horses on the rate of attacks by blood-sucking flies. *Anim Behav* 17:623-625
- Dyer FC (2000) Group movement and individual cognition: lessons from social insects. In: Boinski S, Garber PA (eds) *On the move: how and why animals move in groups*. The University of Chicago Press, Chicago
- Eisenberg J F (1981) *The mammalian radiations: An analysis of trends in evolution, adaptation and behaviour*. University of Chicago Press, Chicago
- Ellard M-E, Crowell-Davis S L (1989) Evaluating equine dominance in draft mares. *Appl Anim Behav Sci* 24:55-75
- Feh C (1988) Social behaviour and relationships of Przewalski's horses in dutch semi-reserves. *Appl Anim Behav* 21:71-87
- Feh C (1999) Alliances and reproductive success in camarque stallions. *Anim Behav* 57:705-713
- Feh C (2001) Alliances between stallions are more than just multimale groups: reply to Linklater & Cameron (2000). *Anim Behav* 61:F27-F30
- Gates S (1979) A Study of home ranges of free ranging Exmoore ponies. *Mamm Rev* 9:3-18
- Geist V (1978) *Life strategies, human evolution, environmental design: Toward a biological theory of health*. Springer Verlag, New York
- Ginsberg JR (1988) Social organisation and mating strategies of an arid adapted equid: The Grévy's zebra. PhD thesis, Princeton University, Princeton, New Jersey, 268 pp
- Goldschmidt-Rothschild Bv, Tschanz B (1978) Soziale Organisation und Verhalten einer Jungtierherde beim Camargue-Pferd. *Z Tierpsychol* 372-400
- Hamilton WD (1971) Geometry for the selfish herd. *Journal of Theoretical Biology* 31:295-311
- Heitor F, do Mar Oom M, Vicente L (2006) Social relationships in a herd of Sorraia horses: Part I. Correlates of social dominance and contexts of aggression. *Behav Processes* 73: 170-177; doi:10.1016/j.beproc.2006.05.004
- Heitor F, do Mar Oom M, Vicente L (2006) Part II. Factors affecting affiliative relationships and sexual behaviours. *Behav Processes* 73: 231-239; doi:10.1016/j.beproc.2006.05.004
- Haupt KA, Wolski TR (1980) Stability of equine hierarchies and the prevention of dominance related aggression. *Equ Vet J* 12:18-24
- Haupt KA, Law K, Martinisi V (1978) Dominance hierarchies in domestic horses. *Appl Anim Ethol* 4:273-283.
- Houston AI, McNamara JM (1988) Fighting for food: a dynamic version of the Hawk-Dove game. *Evol Ecol* 2:51-64
- Huntingford FA, Turner AK (1987) *Animal Conflict*. Chapman & Hall, London
- James R, Bennett PG, Krause J (2004) Geometry for mutualistic and selfish herds: the limited domain of danger. *J theor Biol* 228:107-113
- Jansen T, Forster P, Levine MA, Oelke H, Hurles M, Renfrew C, Weber J, Olek K (2002) Mitochondrial DNA and the origins of the domestic horse. *Proc Natl Acad Sci USA* 99: 10905-10910
- Janson CH (1990) Social correlates of individual spatial choice in foraging groups of brown capuchine monkeys, *Cebus paella*. *Anim Behav* 40:910-21
- Keiper RR (1979) Population dynamics of feral ponies. In: Denniston RH (ed) *Symposium on the ecology and behaviour of wild and feral equids*, 175-184, Laramie: University of Wyoming
- Keiper RR (1988) Social interactions of the Przewalski horse (*Equus Przewalskii* Poliakov, 1881) herd at the Munich zoo. *Appl Anim Behav Sci* 21:89-97
- Keiper RR, Sambaues HH (1985) The stability of equine dominance hierarchies and the effects of kinship, proximity and foaling status on hierarchy rank. *Appl Anim Behav Sci* 16:121-130
- King SRB, Gurnell J (2005) Habitat use and spatial dynamics of takhi introduced to Hustai National Park, Mongolia. *Biol Cons* 124:277-290
- Klimov VV, Orlov VN (1982) Present state and problems of conservation of *Equus przewalskii* Soviet *J Zool* 61:1862-69
- Klingel H (1972) Social behaviour of African equidae. *Zool Afr* 7: 175-186
- Klingel H (1977) Observation on social organization and behaviour of African and Asiatic wild asses (*Equus africanus* and *E. hemionus*). *Z Tierpsychol* 44:323-331
- Kolter L, Zimmermann W (1988) Social behaviour of Przewalski horses (*Equus p. przewalskii*) in the Cologne zoo and its consequences for management and housing. *Appl Anim Behav Sci* 21:117-145
- Krebs JR, Davis NB (2003) *Behavioural Ecology: An Evolutionary Approach* (4th edition). Blackwell Publishing, Oxford, Melbourne, Berlin
- Krueger K (2007) Behaviour of horses in the "Round pen technique". *Appl. Anim. Behav. Sci.* 104, 1-2: 162-170

- Linklater WL, Cameron E (2000) Test for cooperative behaviour between stallions. *Anim Behav* 60: 231-743
- Linklater WL, Cameron EZ, Minot EO, Stafford KJ (1999). Stallion harassment and the mating system of horses. *Anim Behav* 58: 295-306
- McDonnell SM (2003) *The Equid Ethogram: A Practical Field Guide to Horse Behavior*. Eclipse Press, Lexington, Kentucky
- McDonnell SM, Haviland JCS (1995) Agonistic ethogram of the equid bachelor band. *Appl Anim Behav Sci* 43:147-188
- McGregor PK (1993) Signalling in territorial systems: a context for individual identification, ranging and eavesdropping. *Philos Trans R Soc B* 340:237-244
- McGregor PK, Dabelsteen T (1996) Communication Networks. In: Kroodsmas DE, Miller EH, (eds) *Ecology and evolution of acoustic communication in birds*. Cornell University Press, Ithaca, N Y pp 409-425.
- McKnight T (1976) Friendly vermin: A survey of feral livestock in Australia. *Univ Calif Publ Geography* 21:1-104
- Mesterton-Gibbons M, Dugatkin LA (1995) Toward a theory of dominance hierarchies: effects of assessment, group size, and variation in fighting ability. *Behav Ecol* 6:416-423
- Miller R (1979) Band Organisation and Stability in Red Desert Feral Horses. In: Denniston RH (ed) *Symposium on the ecology and behaviour of wild and feral equids*. 113-129, Laramie: University of Wyoming
- Miller R, Denniston RH II (1979) Interband dominance in feral horses. *Z Tierpsychol* 51: 41-47
- Miller RM, Lamb R (2005) *The revolution in horsemanship and what it means to mankind*. The Lyons Press, Guilford, Connecticut.
- Moehlmann PD (ed) (2002) *Equids: Zebra, Asses and Horses. Status Survey and Conservation Action Plan*. IUCN/SSC Equid Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK ix + 190pp
- Moss CJ, Poole JH (1983) Relationships and social structure of African elephants. In: Hinde RA (ed) *Primate Social Relationships: an Integrated Approach*. pp 315-325 Blackwell Science, Oxford
- Naguib M, Fichtel C, Todt D (1999) Nightingales respond more strongly to vocal leaders of simulated dyadic interactions. *Proc R Soc Lond B* 266:537-542
- Nicol CJ 2002 Equine learning: progress and suggestions for future research. *Appl. Anim. Behav. Sci.*, 78:193-208
- Nishida T (1983) Alpha status and agonistic alliance in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Primates* 24:318-336
- Oliveira R F, McGregor PK, Latruffe C (1998) Know thine enemy: fighting fish gather information from observing conspecific interactions. *Proc R Soc Lond B* 265, 1045-1049
- Parker GA (1984) Evolutionary stable strategies. In: Krebs J R and Davis NB (eds) *Behavioural Ecology*, 2nd edn, pp. 30-61. Blackwell Scientific Publication, Oxford
- Paz-y Miño GC, Bond AB, Kamil AC, Balda RP (2004) Pinyon jays use transitive inference to predict social dominance. *Nature* 430:778-781.
- Pollock JI (1980) *Behavioural ecology and body condition change in New Forest ponies*. Horsham, Great Britain: RSPCA Scientific Publication
- Popper KR (1977) Natural Selection and the Emergence of Mind. *Dialectica* 22, 3:339-55
- Pursey AE, Paker C (2003) The Ecology of relationships. In: Krebs J R and Davis NB (eds) *Behavioural Ecology*, 4th edn Blackwell Scientific Publication, Oxford
- Reluga TC, Viscido, S (2005) Simulated evolution of selfish herd behavior. *J theor Biol* 234:213-225
- Rivera E, Benjamin S, Nielsen B, Shelle J, Zanella AJ (2002) Behavioral and physiological responses of horses to initial training: the comparison between pastured versus stalled horses. *Appl Anim Behav Sci* 78:235-252.
- Rubenstein D I (1978) Islands and their effect on the social organisation of feral horses. Paper 100, *Anim Behav Soc Annual Meeting*, Univ Washington, Seattle. June 19.23, 1978
- Rubenstein D I (1981) Behavioural ecology of island feral horses. *Equine Vet J* 13:27-34
- Rutberg AT, Keiper RR (1993) Proximate causes of natal dispersal in feral ponies: some sex differences. *Anim Behav*, 46: 969-975
- Ryder OA, Wedemeyer EA (1982) A cooperative breeding programme for the Mongolian wild horse, *Equus przewalskii* in the United States. *Biol Cons* 22:259-271
- Salter RE.(1979) Biogeography and Habitat-use Behavior of Feral Horses in Western and Northern Canada. In: Denniston R H (ed) *Symposium on the ecology and behaviour of wild and feral equids*. 129-141, Laramie: University of Wyoming
- Salter RE, Hudson RJ (1982) Social organisation of feral horses in western Canada. *Appl Anim Ethol* 8:207-223
- Schilder MBH (1990) Intervention in a herd of semi-captive plains zebra. *Behaviour* 112: 53-83
- Sighieri C, Tedeschi D, de Andreis C, Petri L, Baragli P (2003) Behaviour patterns of horses can be used to establish a dominant-subordinate relationship between man and horse. *Animal Welfare* 12:705-708
- Tyler SJ (1972) The behaviour and social organisation of the new Forest ponies, *Anim Beh Monog* 5:85-196

- U S Bureau of Land Management (BLM) (2006) U.S. Department of the Interior, Office of Public Affairs
- Viscido SV, Miller M., Wethey DS (2001) The Response of a Selfish Herd to an Attack from Outside the Group Perimeter. *J theor Biol* 208:315-328
- Viscido SV, Miller M, Wethey DS (2002) The Dilemma of the Selfish Herd: The Search for a Realistic Movement Rule. *J theor Biol* 217:183–194
- Welsh DA (1975) Population, behavioural, and grazing ecology of the Sable Island, Nova Scotia Ph. D. Diss. Dalhousie University
- Waring GH (1979) Behavioral Adaptions as a Factor in the Management of Feral Equids. In: Denniston RH (ed) Symposium on the ecology and behaviour of wild and feral equids. 85-92, Laramie: University of Wyoming
- Zervanos SM, Keiper RR (1979) Seasonal home ranges and activity patterns of feral Assateague Island ponies. In: Denniston RH (ed) Symposium on the ecology and behaviour of wild and feral equids. Laramie: University of Wyoming