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 encounter 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, Hamiltons (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 strategy 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 extend. 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 thought 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 live. 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 then 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 Cameroon 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 byremoval 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 Sambraus 1985, Linklater et al. 1999), both traits, which are uncorrelated with RHP (Pursey and Paker 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 coincidently 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 of 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 correles 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 coincidently 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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