

On the development of social behaviour in immature males of a feral horse population (*Equus przewalskii* f. *caballus*)

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Abstract

Social behaviour was observed for two consecutive years in all maturing individuals of a feral horse population on an island off the coast of North Carolina, USA. The ontogeny of social behaviour was examined with regard to age, sex and social environment and compared with the social behaviour of adult horses. Both frequency and structure of behaviour patterns differed between the sexes after the first year of life; these differences increased with age until both sexes had attained adulthood. Male horses spent most of their first five to six years of life in the bachelor group. The quantitative and qualitative development was dependent both on social context and age. Young males remaining in their mothergroup until sexual maturity were less active and showed fewer different social patterns than their peers in the bachelor group. The same was true for sexually mature bachelors trying to form their own female group before they had reached the age of five years. In any age period the total number of different behaviour patterns of all horses was at least twice the number of different patterns observed in a single horse; both were highest in sexually mature bachelors. Apparently the bachelor group serves to promote the individuals' social development and practice of role-specific behaviour in a non-serious environment.

Introduction

Recent studies of feral and wild Equid populations have paid particular attention to social behaviour and organization. Plains zebra (*Equus quagga boehmi*) and Mountain zebra (*E. zebra hartmannae*) as well as feral horses (*Equus przewalskii* f. *caballus*) generally live in female-offspring groups dominated and defended by one stallion, with associated bachelor groups (IMANISHI 1953; MCKNIGHT 1958; BRUEMMER 1967; KLINGEL 1969, 1972, 1974; RHYMER 1970; FEIST 1971; JOUBERT 1972; TYLER 1972; WELSH 1973; BERGER 1977; MILLER and DENNISTON 1979; HOFFMANN 1980). The social system of Grevys' zebra on the other hand seems to be related to the systems of wild asses (*E. hemionus*, *E. africanus*) and feral asses (*E. africanus* f. *asinus*) (KLINGEL 1974; MOEHLMAN 1974; WOODWARD 1978; HOFFMANN 1983a). Neither have harem-like groups. Adults live singly or in mother-offspring groups. However, temporary assemblages of all kinds occur frequently. In some populations males will establish large territories during the breeding season which are defended only against other males in the presence of estrous females. Of all equids horses appear to be the most flexible species. Recent studies revealed possibly territoriality (RUBENSTEIN 1981; POLLOCK pers. comm.), mixed-sex peer groups (KEIPER 1976a; VON GOLDSCHMIDT-ROTHSCHILD and TSCHANZ 1978) and even a totally loose social system comparable to the system of feral asses (HOFFMANN 1983a). Aside from their type of social organization, all known equid species have a surprisingly uniform set of basic social behaviour patterns which they use in similar social contexts (KLINGEL 1972). In all Equid species males are physically able to and frequently do dominate females and offspring

independently of their social organization (BERGER 1983). Especially in horses organized in harem groups the reproductive success of a population may be totally dependent on the male's social, environmental and spatial strategy. Group stallions defend their mares and valuable resources such as waterholes or food patches against other stallions and bachelor males (KLINGEL 1972; RUBENSTEIN 1981; HOFFMANN 1983b) and they may sire most of the offspring in their harem group (HOFFMANN 1983b). A mare's social activity usually is restricted to mother-foal interaction and few social contacts with the other harem mares (FEIST and McCULLOUGH 1976; HOFFMANN 1980, 1983; WARING 1983; and others).

The development of two different sex-related roles in Equids is not yet completely understood. In feral horses both male and female foals spend the first year of their life in close contact with their mother and her group (TYLER 1972; KLINGEL 1972; VON GOLDSCHMIDT-ROTHSCHILD and TSCHANZ 1978; HOFFMANN 1983b). In one studied population most foals left their maternal group between the first and second breeding season (HOFFMANN 1983b). Most of the female foals are sexually receptive when they are between one and two years old (KLINGEL 1972; WARING 1983, and others) and then join other harem groups (FEIST 1971; TYLER 1972; HOFFMANN 1980; and others). Young males live in unstable bachelor groups until they are five to six years old (ALVERDEZ 1925; KLINGEL 1964, 1965; FEIST 1971; BERGER 1977; HOFFMANN 1980, 1983). They enter the reproductive stage of their life considerably later than do females. On the other hand male and female foals of the investigated feral island population did not differ significantly in their observable social behaviour and activity (HOFFMANN 1983), and reports of the other feral horse populations indicate the same result (FEIST and McCULLOUGH 1976; BERGER 1977). Therefore it should be assumed that in feral populations the development of the complex social behaviour of males takes place during bachelorhood, i.e. the period they spend in bachelor groups.

Material and methods

This project was conducted with a population of feral horses on Bird Shoal-Carrot Island off the US coast of North Carolina, USA. The population originates from another feral horse population on adjacent Shackleford Island, lives completely undisturbed by man and has no natural enemies. The island, a narrow complex of salt marsh, intertidal sand and mud flats, creeks, dredge spoils and patches of maritime forest, is approximately 6 km long, between 0.5 and 1 km wide and is uninhabited by man. Approximately 30% of the total area of the island is covered by salt marsh (*Spartina alterniflora*); which also comprises the main diet of the horses (HOFFMANN 1982; LIN 1982). Freshwater occurs naturally only after heavy rains, gathering in pools formed by dredge spoils. Normally the only other source of fresh water are holes dug and maintained by the horses. During the summer, water in these holes is very scarce and in dry seasons turns brackish (HOFFMANN 1980). There are no other large herbivorous mammals found on the island. The climate is subtropical.

The social organization and population dynamics of the studied horse population did not differ from other feral horse populations (HOFFMANN 1982): non-territorial, stable groups of one to four mares were dominated by one stallion throughout the year. Over the study period several two-male harem groups formed, with one dominant, driving and reproducing male and one subdominant male at the group periphery. The breeding season lasted from mid April until June/July: thus most of the foals were born within a four to six week range. The population grew almost linearly from 24 horses observed in 1977 to 50 horses in 1982, with a sex ratio varying between an even ratio and 1.4 males to 1 female.

Observation modus

At the beginning of every observation day the island was systematically scanned for horses from one end to the other. No night observations were conducted. The location, identity, group composition and activity was recorded for every individual. The identity and genetic background (mother and, for some animals, the group stallion as possible father) of every horse younger than 5 years was known from previous studies on the same population in 1977-1978 (HOFFMANN 1980). Individuals and groups were followed as long as possible, on some occasions (e.g. in flooded saltmarshes) by boat. The frequency of every social behaviour pattern, the partner of exchange and the response was continuously marked on prepared data sheets, usually for one observation hour; the social and environmental context was described and recorded.

From September 1980 until March 1981 all bachelors aged one to five years were observed, from March 1981 until July 1982 all other horses on the island were included. Thus all bachelors on the island were observed for two nonbreeding seasons (Sept. 80–March 81; August 81–March 82) and two breeding seasons (March 81–July 81; March 82–July 82). A total of 6752 hours of behavioural observation was accumulated over the two years. Of this total, 4253 hours were spent on male foals and bachelors aged 0–62 months ($n = 22$), and 822.5 hours on adult males ($n = 8$).

Definitions

Behaviour

In order to measure the frequency of social behaviour behavioural events had to be classified: I defined the smallest observable unit of behaviour as a behavioural stereotype, such as "ear position up". A behaviour pattern was defined as a single stereotype or (one and only one) combination of stereotypes. Every new combination of stereotypes, even if it occurred only once was regarded as a new behaviour pattern. Patterns with apparently common underlying meanings, stimuli and results were grouped into one behavioural category and labeled accordingly. The intensity of the pattern was measured by the reaction of the opponent. During a two month pilot study all stereotypes and patterns occurring in the population were identified and compared with the observations and descriptions in the literature (ANTONIUS 1939; GRZIMEK 1944; ZEEB 1958, 1959; TRUMLER 1959; FEIST 1971; TYLER 1972; CLUTTON-BROCK 1976; WELLS and v. GOLDSCHMIDT-ROTHSCHILD 1978). All observed behaviours are listed in the Table.

Age

The occurrence and frequency of behaviour patterns and categories was related to age. The age of bachelors was expressed in time periods equivalent to the different seasons in the study. Therefore, the age periods used have two different lengths: eight months (nonbreeding season) and four months (breeding season). The data obtained from observations of horses of the same age, but in different seasons, were put together into the same age period.

Social Context

I defined two generally different social contexts for male horses: a. permanent contact with females, and b. no permanent contact with females. The first context applied to 1. immature males in their mothers' group called mothergroup bachelors, 2. sexually mature bachelors which temporarily kept females (called harem group bachelors) and 3. adult stallions with a harem group.

Statistical evaluation

Every observed behaviour pattern was counted as one event. The frequency of occurrence of every single pattern was standardized for every individual as n events/observation hour per age period (= season). With paired data, I applied the Sign test, Wilcoxon matched pairs signed-ranks test or Walsh test, nonpaired data were analyzed with the Man-Whitney U-Test (SIEGEL 1956).

Results

First occurrence of behaviour patterns

Male horses on the island used a total number of 58 different behaviour patterns, most of which had role-specific or sex-specific character (see Table). Driving, complete forms of both urine marking and defecation marking and complex agonistic patterns were not observed in immature animals and adult females. Playing behaviour patterns as described in Table 1 were almost never observed in adult animals. In young males it was by far the most commonly observed social behaviour. The majority of male foals and yearlings used the low-key playing patterns 39, 6a and 9a. The high intensity patterns (11a, 12a) were not observed to occur before the third year of life, and then, only in very few males. Both the number of different playing patterns used and the intensity of play increased with age and peaked at the age of 34–50 months and decreased thereafter.

Behaviour categories, their individual patterns and labels, of male horses on Bird Shoal-Carrot Island

Category	Label	Sequence of stereotypes (Pattern)			
Greeting	0	Ears up; naso-nasal contact	Defecation	20	Sniff
	1	Ears flat back; naso-nasal contact	Marking	21	Sniff fresh pile
Grooming	40	Ears up; initiating; allo-grooming		25	Sniff old pile
	41	Ears up; initiating; mutual grooming		21b	Sniff fresh pile; defecate
	42	Ears up; passive mutual grooming		25b	Sniff old pile; defecate
				22	Sniff fresh pile; marking position
				26	Sniff old pile; marking position
Playing Behaviour	39	Ears up; initiating		23	Sniff fresh pile; marking position; defecate
	42a	Ears up; snap; wrestle; groom		27	Sniff old pile; marking position; defecate
	6a	Ears up; chase		24	Sniff fresh pile; marking position; defecate; 180° turn; sniff own mark
	9a	Ears up; bite		28	Sniff old pile; marking position; defecate; 180° turn; sniff own mark
	10a	Ears up; front hoof beating			
	11a	Ears up; front hoof beating; bite			
Submissive Behaviour	12a	Ears up; front hoof beating; bite; chase			
	13	Ears flat back; stretch neck; teeth blecking	Urine Marking	37	Flehmen
	14	Ears flat back; stretch neck; teeth clapping		29	Sniff urine
	15	Ears up; walk away		33	Sniff urine; flehmen
	16	Ears flat back; run away		30	Sniff urine; marking position
Agonistic Behaviour	3	Ears flat back; (treath)		31	Sniff urine; marking position; urinate
	4	Ears flat back; naso-nasal contact; head beating		34	Sniff urine; marking position; urinate; flehmen
	4b	Ears flat back; head beating-movement		32	Sniff urine; marking position; urinate; 180° turn; sniff own mark
	5	Ears flat back; naso-nasal contact; head beating; vocalization		35	Sniff feces; flehmen
	6	Ears flat back; chasing		38a	Sniff feces; marking position; urinate
	7	Ears flat back; snap		36	Sniff feces; flehmen; urinate
	8	Ears flat back; hindhoof kick; vocalization	Driving Behaviour	17	Ears flat back; stretch neck; chase
	9	Ears flat back; bite		18	Ears back; drive
	10	Ears flat back; front hoof beating; vocalization			
	11	Ears flat back; front hoof beating; bite; vocalization	Sexual Behaviour	47	Ears flat back; sniff female genitals
	12	Ears flat back; front hoof beating; hindhoof kick; chase; vocalization		48	Ears flat back; sniff female genitals
				51	Ears flat back; courting female; vocalization
			49	Ears up or flat back; mounting female	
			50	Ears up or flat back; copulation with female	

Over the entire study period only 20–30% of all adult animals showed grooming behaviour. While young bachelors used all three patterns of grooming, sexually mature bachelors after the age of four years did not groom at all, with possibly one exception.

Most of the agonistic patterns developed significantly later in life. The first behaviour patterns with agonistic character in male foals were simple, low-key deensive patterns (7, 8 and 3). The other agonistic patterns appeared successively in the second and third year of

life, usually in very few horses at the beginning. Again, just as in playing behaviour the intensity and pattern complexity correlated with the sequence of first occurrence. At the age of 50–58 months all adult bachelors used almost all agonistic behaviour patterns, just as group stallions did. The agonistic patterns 9, 10, 11 and 12 are identical in their composition and sequence of stereotypes with the playing patterns 9a, 10a, 11a, and 12a, except for ear position and vocalization. The time of first occurrence of these agonistic patterns was preceded by the first occurrence of the equivalent playing patterns by one to two seasons. The occurrence of patterns 12 and 12a had a seasonally alternating character: in the breeding season 12 was high and 12a low, in the nonbreeding season 12 was low and 12a high.

Adult stallions showed only complete forms of defecation marking. The occurrence of the incomplete forms in bachelors was age-related: All male foals reacted to olfactory stimuli (sniff pile). Some yearling males did use the upright marking position typical for adult males after sniffing a pile, but did not defecate. Two year old males showed both types of behavioural "precursors" (21, 22), and in their third breeding season all types of precursors and complete marking was observed. Thereafter incomplete forms of marking were abandoned.

Male horses marked both female feces and female urine with their own urine. Both forms of urine marking, as well as flehmen in combination with olfactory investigation of urine and feces were observed to occur already in some male foals. Three year old bachelors used all different combinations of urine marking, as did adult stallions.

Three female-oriented behaviour patterns with sexual character appeared in male foals (47, 48, 49). Two yearlings courted a female, but copulation and driving was not observed to occur before the third breeding season. All of the observed patterns with sexual character and driving were directed against females only, except for several instances of mounting in bachelor play. The first occurrence and the number of animals using driving and sexual behaviour was dependent on the presence of females.

Most of the more complex behaviour patterns of play, agonistic behaviour, and both forms of marking appeared for the first time in only one or two horses of an age class. It then took 1½ to 2 years until all males of this age group had displayed this pattern.

Total social activity

The total frequency of the social activity in adult horses varied between 0.3 and 0.5 events/h in mares and 2 and 3 events/h in stallion (Fig. 1). In both sexes it was lower in the nonbreeding season than in the breeding season (for males $p \leq .01$, Wilcoxon). The social activity of male foals increased during the first 14 months, but then decreased to the lowest value of the male socialization period at age 14–22 months. Young males then became increasingly more active reaching the adult male level at the age of 3 years. The frequency distribution of the total social activity showed strong seasonal character in immature males.

Absolute frequency of behaviour categories

The average absolute frequency of occurrence of a category was expressed as the arithmetic mean with standard deviation of all individual events per hour in one age group (Fig. 2). The most frequently observed social behaviour category in stallions was agonistic behaviour (0.74–1.3 events/h), followed by defecation-marking (0.37–0.54 events/h) and driving (0.28–0.50 events/h). Together these activities comprised roughly 2/3 of the total events. There was no significant difference observed in the frequency of these activities between the breeding and nonbreeding seasons. Sexual behaviour and urine marking occurred significantly more often ($p \leq .017$ Mann-Whitney U-test) in the breeding season. In adult stallions both playing and grooming behaviour were the least observed social

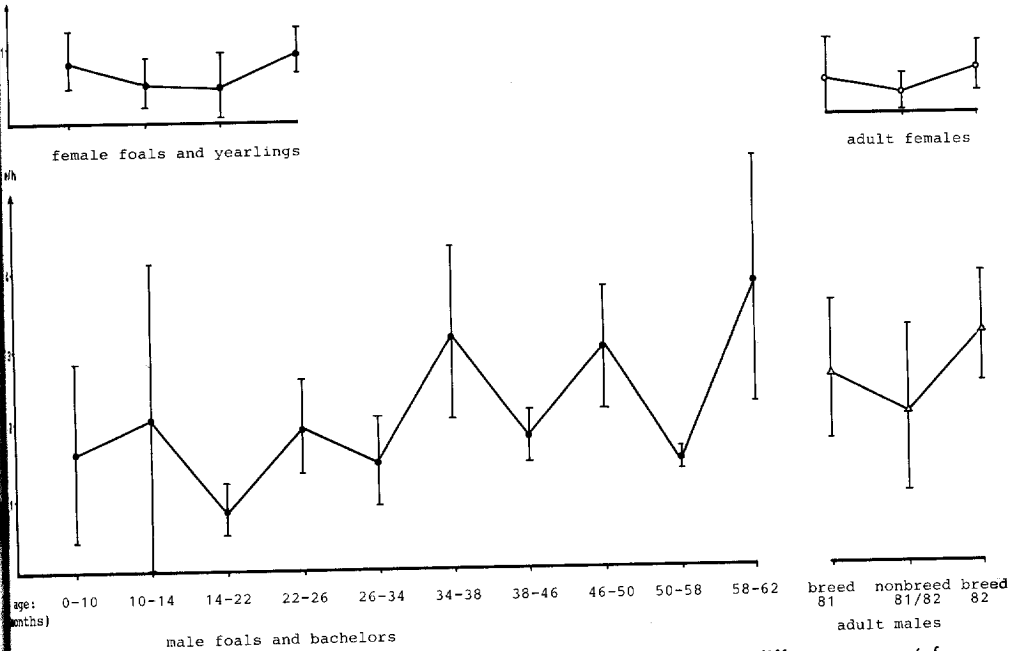


Fig. 1. Average social activity of horses over age (of immature animals) and in different seasons (of adult animals). One value represents the mean total number of social events/hour of one horse in the given age period, with standard deviation. Symbols: male foals and yearlings: ●, female foals and yearlings: ●, adult males: Δ, adult females: ○

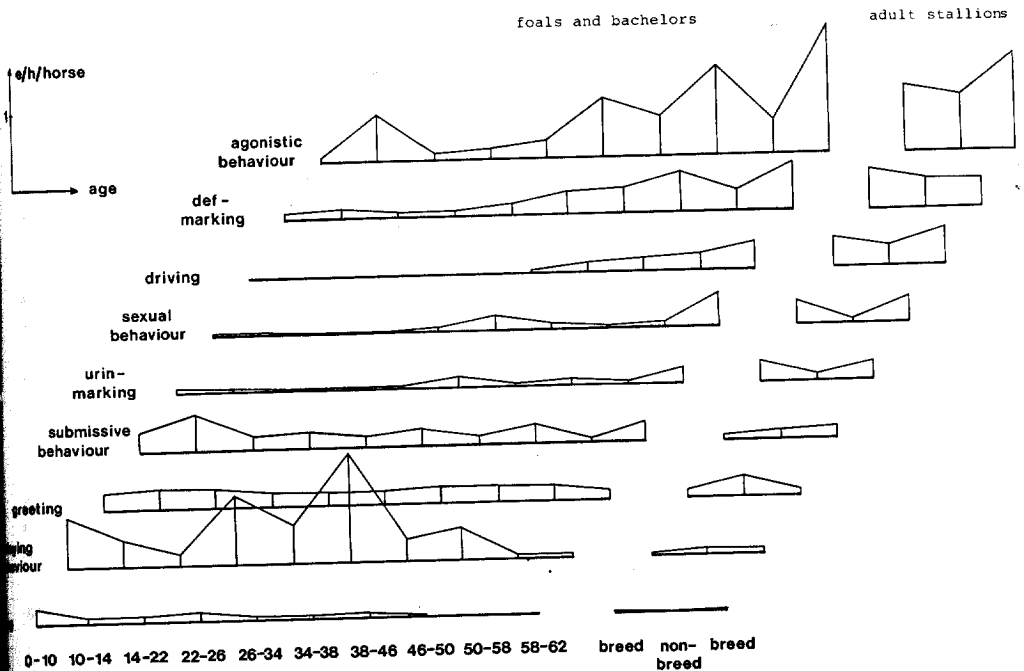


Fig. 2. Quantitative distribution of social behaviour over age: absolute frequency of individual behaviour categories in one horse, in events/hour, in different age periods and seasons

activities. Greeting was a frequently observed way of establishing contact, but only in the nonbreeding season.

A comparative examination of the frequency distribution over age in young males reveals at least 3 different maturation periods:

Age 0–22 months: The frequency of the social activity was fairly evenly distributed over the categories grooming, play, greeting and submission; both forms of marking, as well as sexual behaviour, was used only sporadically. Except for during the first breeding season, agonistic behaviour occurred less often than any of the nonagonistic and marking behaviours. The highest frequency of grooming at any age occurred in foals.

Age 22–38 months: At this age, just before reaching sexual maturity, playing behaviour was by far the most frequently observed social behaviour in young males. The frequency of grooming and submission decreased with age, whereas the frequency of marking, agonistic behaviour and sexual activity began to increase slowly. Driving occurred first after sexual maturity, which was attained between the age of 26 and 38 months.

Age 38–62 months: Between the 38th and 62nd month of life, the whole set of behaviour categories gradually shifted into the adult male frequency distribution type. Frequencies of nonagonistic categories such as play behaviour, grooming and greeting continuously decreased, whereas behaviour patterns of the other categories were used more frequently. Bachelors trying to build up their own harem group (age 46–50 months) for the first time used significantly more agonistic ($p \leq .031$; Mann-Whitney U-test) and submissive behaviour ($p \leq .045$; Mann-Whitney U-test) than adult stallions. At the same age, the bachelors still played more than adult stallions.

Generally agonistic and submissive behaviour and, after maturity, urine marking was observed more often to be used in the breeding season than in the nonbreeding season. Playing behaviour showed strong seasonality only during its peak frequency (age 22–38 months). The development of all other behaviour categories in bachelors was seasonally independent.

Relative frequency of behaviour categories

Every animal had its own specific distribution of behaviour category frequencies within its total social activity. This distribution varied with age. The combined relative frequency distributions within one age period reveal how much of its total social activity an animal of this age will actually spend on certain behaviours, such as agonistic behaviour. The mean distributions over age are then compared between the different types of bachelors.

Male foals which had left their mother group at the age of 10–14 months spent a significantly higher amount of their social activity on agonistic behaviour ($p \leq .026$; Mann-Whitney U-test) and submissive behaviour than male foals remaining in their mothergroup (Fig. 3). These two behaviours accounted for almost 90% of the total social activity in yearling bachelors. During the age periods of 22–26 months and 26–34 months the situation was reversed. Mothergroup bachelors were relatively more submissive than bachelors, and significantly more aggressive during the nonbreeding season, at the age of 26–34 months ($p \leq .072$ Mann-Whitney U-test). Sexually mature bachelors in association with females spent a higher percentage of their social activity on agonistic encounters ($p \leq .07$ Sign) and significantly less on submissive behaviour ($p \leq .019$ Sign) than when they were just bachelors. In adult stallions the correlation between female presence and relative frequency of agonistic behaviour was reversed: stallions which had lost their group spent a higher proportion of their total activity on both agonistic and submissive behaviour than harem group stallions.

The relative frequency of defecation marking in young males increased with age, but there were no context related frequency changes.

Urine marking filled only a small part of the bachelors' social "budget". Only in sexually mature bachelors with permanent contact with females did urine marking become

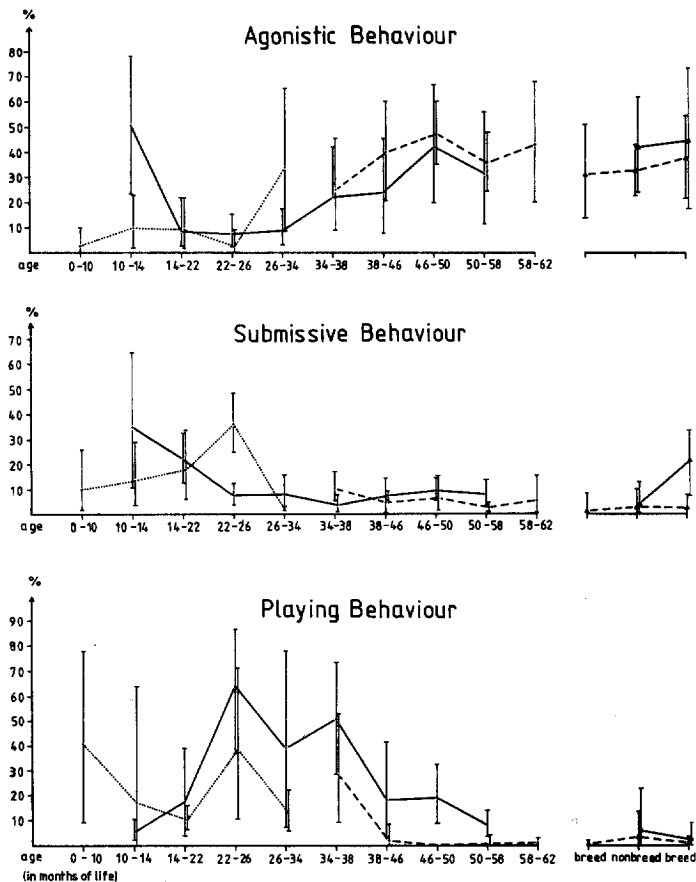


Fig. 3. Relative frequency of behaviour categories, within one age group, over age in males: one value represents the mean relative frequency of all pattern of this particular category, in relation to total social activity, in this age group, derived from all individual distributions of the members of this age group. Symbols: bachelors: ●—●, mothergroup bachelors: ●·····●, harem group bachelors: ●- - -●, stallions with harem groups: Δ- - -Δ, single stallions: ▲—▲

a frequently used activity (5% of the total activity); while being a bachelor, the same horse showed no urine marking at all.

Playing behaviour comprised up to 60% of the social behaviour in bachelors and was strongly context dependent in its relative frequency. Mothergroup bachelors spent significantly less of their social activities on play than bachelors of the same age (14–22 months: $p \leq .017$; 22–26 and 26–34 months: $p \leq .07$; Mann-Whitney U-test). Males at the age of 46–50 months did not play at all when being a harem group bachelor, but did spend 18% of their social activity on play as “real” bachelors.

Absolute and relative variability of patterns

There were no horses which in any given season or age period showed all the behaviour patterns that had been observed to occur in their sex on the island. Furthermore there were no age periods or seasons in which I observed all patterns occurring on the island. Therefore in order to gain some understanding of the behavioural flexibility of the animals

in this population, it seemed appropriate to investigate the difference between the total number of different behaviour patterns occurring in one age period (absolute variability) with the actual mean number of different behaviour patterns observed in one horse this age (relative variability). If the horses of a certain age period used the same number, but different types of behaviour patterns, their individual flexibility (relative variability) had to be smaller than the age period specific flexibility (absolute variability).

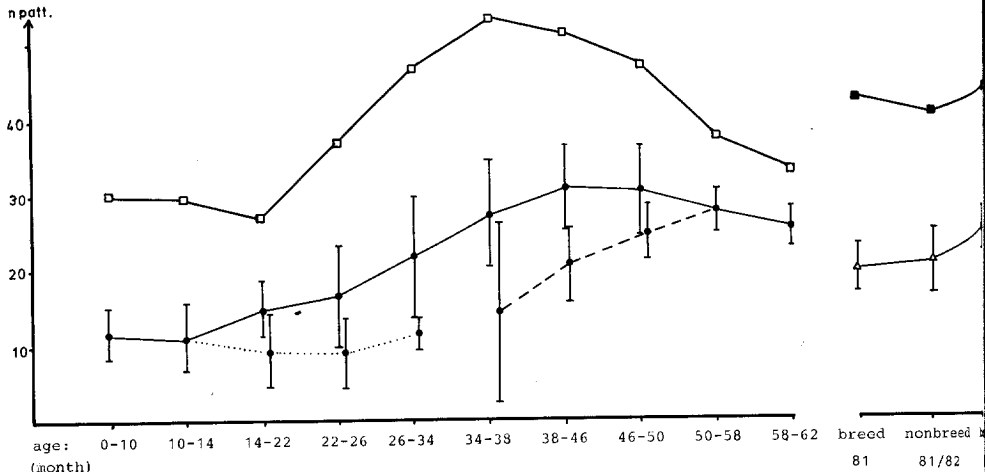


Fig. 4. Absolute and relative variability of social behaviour in males: absolute variability is the total number of different patterns used in one age period or season, by all horses together; symbols: absolute variability of bachelors: □, absolute variability of stallions: ■; relative variability is the mean of the total number of different patterns observed in one horse in one age period. Symbols: bachelors: ●—●, mothergroup bachelors: ●·····●, harem group bachelors: ●---●, stallions: △—△

The absolute variability of immature males was lowest in foals and yearlings (Fig. 4). It rose to a high value of 54 different patterns in the age group of 34–38 months, and then decreased to 33 patterns for the period of 58–62 months. Generally, the absolute variability of mature bachelors was lower than in adult stallions, and did not show seasonality as the adult values did. The absolute variability was twice as high as the relative variability.

The development of the relative variability in bachelors was quite different. It increased from a low value of 12 patterns in foals and yearlings to a high value of 30 at 38–46 months, and then decreased slightly to the level of adult males by the age period of 58–62 months. The relative variability in harem group bachelors aged 46–62 months was significantly higher than in adult males (breeding season 81: $p \leq .0015$; nonbreeding season: $p \leq .02$; Mann-Whitney U-test).

The relative variability of mothergroup bachelors was much lower than the relative variability of true bachelors, and never reached their values within one age group. After sexual maturity the values of harem group bachelors, which at the third breeding season (age 34–38) had been the lowest of this age group, increased and reached adult male levels at 38–46 months, but, again, never the values of bachelors of the same age. In general contact with females decreased the number of different behaviour patterns within a given age period in immature males.

Discussion

Although many studies have been conducted on ontogenetic aspects of domestic foals (GRZIMEK 1949; WARING 1970, 1972, 1983; WILLIAMS 1974; FAGEN and GEORGE 1977;

BOY and DUNCAN 1979; FRASER 1980; FAGEN 1981), only few quantitative data are available on aspects of the development of social behaviour in truly feral horse populations. The first occurrence, sequence and frequency of behaviour patterns in New Forest foals (TYLER 1969) differed from the foals of my study population. New Forest foals not only nursed and rested more, they also seemed to groom and play much more with each other and with subadult and adult animals. This was also reported for Camargue foals (WELLS and v. GOLDSCHMIDT-ROTHSCHILD 1979). This may have been due to the social organization of New Forest ponies and Camargue horses: the number of potential socialisation partners (peers) within a group was higher for foals. While foals in the studied population seemed to lack the opportunity to establish social contacts, they first of all developed those nonagonistic and low-key agonistic patterns normally used by adults to regulate the social relations within a harem group. Thus the actual frequency of practicing group-stabilizing behaviour in immatures seemed of little importance to the population, because its social structure, group stability, and reproductive success was not different from other feral horse populations (HOFFMANN 1980, 1983b).

The similar development of social noncompetitive patterns in foals of both sexes was followed by a strong role-specific split in the ontogeny over the next four years of age. Young sexually immature bachelors spent most of their time playing, when they had joined the bachelor group. In other equids, such as the mountain zebra (JOUBERT 1972), feral asses (WOODWARD 1979), domestic horses (FAGEN 1981; WARING 1983), and semi-feral populations (TYLER 1972), playing behaviour seemed to be the main social activity also. Unlike the bachelors on Bird Shoal-Carrot Island, the play in foals and yearlings of the Camargue and New Forest populations already contained agonistic elements. This seems quite surprising and I cannot readily explain this difference. Probably the presence of a dominant stallion in Bird Shoal-Carrot Island groups suppressed every behaviour with competitive elements. FEIST (1971) observed a similar control of social play in immature group members by the stallion. This may also explain the differences between bachelors and same-aged mothergroup bachelors. In the latter, the absence of same aged peers and the constantly serious environment forcefully reduced the individual flexibility, choice and proper application of adult male-specific behaviour patterns. On the other hand, most of the new behaviour patterns occurred first in males in contact with adult females. I therefore assume that many stimuli for the first appearance of patterns may lie in the social environment of a harem group. The actual practice and application in the proper context was possible though only in a social environment free of serious competition.

Camargue and New Forest males were observed to reproduce following sexual maturity, depending on the time of year (TYLER 1972; WELLS and v. GOLDSCHMIDT-ROTHSCHILD 1979). Sexually mature bachelors on Bird Shoal-Carrot Island were not able to reproduce until their fifth or sixth year of life. This intermediate state of development between sexual maturity and behavioural maturity was also reported by FEIST (1971) for the Pryor Mountain horses, and by KLINGEL for Grant's zebra, Plains zebra and even the territorial Grevy zebra (1965, 1969, 1972). Although few data are available on feral ass bachelors, preliminary observations indicate that adult, dominant males temporarily accompanying estrous females prevent young males from mating (HOFFMANN 1983a).

Delayed onset of male reproduction is widespread in polygynous species (e.g. elephant seals: LE BOEUF 1974; antelopes: JARMAN and JARMAN 1974, GOSLING 1974; and others) and in species with female family units and peripheral males (e.g. primates: v. LAWICK-GOODALL 1968; MARTIN 1972; CHARLES-DOMINIQUE 1972; and others). In the observed horses, the time span between physical and actual reproductive status apparently served to provide a male with the role-specific skills necessary to build up, maintain and successfully defend the core reproductive unit with its offspring. This was demonstrated by the gradual shift of the occurrence, frequency and flexibility of social behaviour from the bachelor set to the adult male set. As well as in immature bachelors this shift was altered by the presence

of females, but, contrary to immature bachelors the differences between bachelor status and harem group status decreased with increasing age.

In concluding, it appears that male horses go through several age-related phases of development, with behaviour sets characteristic in their structure, frequency distribution and type of development. According to WILEY (1980), these phases could also be regarded as functional positions in the given society. Transitions from an early position into the next position occurred in all males and were always irreversible, measured by the occurrence, frequency and variability of their behaviour. On the population level, I propose that functionally the bachelor group on Bird Shoal-Carrot Island resembles the lek system found in other herbivorous mammals (ESTES 1969; BUECHNER and ROTH 1974). A lek system may provide males a possibility of progression in rank and position towards a reproductive state. On Bird Shoal-Carrot Island, all immature males proceeded through the various bachelor positions until they had reached reproductive age.

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Zusammenfassung

Über die Entwicklung des Sozialverhaltens von heranwachsenden Hengsten einer verwilderten Pferdepopulation (Equus przewalskii f. caballus)

Bei allen heranwachsenden Tieren einer verwilderten Pferdepopulation, die auf einer, der Küste von North Carolina, USA, vorgelagerten Insel lebt, wurde das soziale Verhalten über den Zeitraum von zwei Jahren beobachtet. Die Entwicklung des Sozialverhaltens der Jungtiere wurde in Bezug zu Alter, Geschlecht und sozialem Umfeld gesetzt.

Die Häufigkeit des Auftretens und die Struktur der sozialen Verhaltensweisen waren nach dem ersten Lebensjahr in beiden Geschlechtern unterschiedlich; die geschlechtsspezifischen Unterschiede verstärkten sich mit zunehmendem Alter. Die meiste Zeit der ersten fünf bis sechs Lebensjahre verbrachten Junghengste zusammen mit anderen Junggesellen. Ihre Verhaltensentwicklung war quantitativ und qualitativ abhängig vom sozialen Umfeld und vom Alter. Junghengste, die bis zur sexuellen Reife in der Muttergruppe bleiben, zeigten weniger Aktivität und weniger Flexibilität (verschiedene Verhaltensweisen) als gleichaltrige Junggesellen in der Junggesellengruppe. Dies traf auch zu für sexuell reife Junggesellen, die versuchten, eine Haremgruppe aufzubauen, bevor sie fünf Jahre alt waren.

In jeder Altersstufe war die Anzahl aller beobachteten Verhaltensweisen mindestens doppelt so groß wie die in jedem einzelnen Tier dieser Altersstufe beobachteten verschiedenen Verhaltensweisen. Erwachsene Junggesellen zeigten die größte Anzahl verschiedener Verhaltensweisen.

Alle Junggesellen durchliefen jedoch – früher oder später – die verschiedenen, durch qualitative und quantitative Verhaltensparameter voneinander abgrenzbaren Stadien der Verhaltensentwicklung. Diese Entwicklung war irreversibel: Junggesellen, die einen bestimmten Status erreicht hatten, kehrten nie wieder auf ein früheres Stadium zurück. Funktionell dient die Junggesellengruppe der harem bildenden Equiden wahrscheinlich der Entwicklung und dem Einüben rollenspezifischer Verhaltensweisen in nicht-ernster Umgebung.

References

- ANTONIUS, O. (1939): Über Symbolhandlungen und Verwandtes bei Säugetieren. *Z. Tierpsychologie* 3, 263–278.
- BERGER, J. (1977): Organizational Systems and Dominance in Feral Horses in the Grand Canyon. *Behav. Ecol. Sociobiol.* 2, 131–146.
- BERGER, J. (1983): Induced Abortion and Social Factors in Wild Horses. *Nature* 303, 59–61.
- BOY, V.; DUNCAN, P. (1979): Time-budgets of Camargue Horses I: Developmental Changes in the time budgets of foals. *Behaviour* 71, 187–202.
- BRUEMMER, F. (1967): The wild horses of Sable Island. *Animals (London)* 10, 14–17.

- BUECHNER, H. K.; ROTH, H. D. (1974): The Lek System in Uganda Kob Antelope. *American Zool.* **14**, 145-162.
- CHARLES-DOMINIQUE, P. (1972): Ecologie et vie sociale de *Galago demidovii* (Fischer 1808, Prosimii). *Fortschritte der Verhaltensforschung* **9**, 7-41.
- CLUTTON-BROCK, T. H.; GREENWOOD, P. J.; POWELL, R. P. (1976): Ranks and Relationships in Highland Ponies and Highland Cows. *Z. Tierpsychol.* **41**, 202-216.
- ESTES, R. D. (1969): Territorial Behaviour of the Wildbeest (*Connochaetus taurinus*) *Z. Tierpsychol.* **26**, 284-370.
- ESTES, R. D. (1974): Zebras offer clues to the way wild horses once lived. *Smithonian* **5**, 101-107.
- FAGEN, R. M.; GEORGE, T. K. (1977): Play Behavior and Exercise in Young Ponies (*Equus caballus*). *Behav. Eco. Sociobiol.* **2**, 267-269.
- FAGEN, R. M. (1981): *Animal Play Behavior*. Oxford University Press.
- FEIST, J. D. (1971): Behavior of Feral Horses in the Pryor Mountain Wild Horse Range. Master Thesis, University of Michigan.
- FEIST, J. D.; MCCULLOUGH, D. R. (1976): Behavior Patterns and Communication in Feral Horses. *Z. Tierpsychol.* **41**, 337-371.
- FRASER, A. F. (1980): The Ontogeny of Behaviour in the Foal. *Appl. Anim. Ethol.* **61**, 303-308.
- GOLDSCHMIDT, B.; TSCHANZ, B. (1978): Soziale Organisation und Verhalten einer Jungtierherde beim Camargue-Pferd. *Z. Tierpsychol.* **46**, 372-400.
- GOSLING, L. M. (1974): The Social Behaviour of Coke's Hartbeest (*Alcelaphus buselaphus cokei*). In: *The Behavior of Ungulates and its Relation to Management*. Ed. by V. GEIST and F. WALTER. Morges, Switzerland.
- GRZIMEK, B. (1944): Rangordnungsversuche mit Pferden. *Z. Tierpsychol.* **6**, 455-464.
- GRZIMEK, B. (1949): Ein Fohlen, das kein Pferd kannte. *Z. Tierpsychol.* **6**, 391-405.
- HOFFMANN, R. (1980): Soziale Strategien einer Population von verwilderten Pferden (*Equus caballus*) auf einer Insel in North Carolina, USA. Master Thesis, Universität Tübingen, FRG.
- (1982): Management Plan for the Feral Horse Population on Bird Shoal-Carrot Island, North Carolina. North Carolina Nature Conservancy.
- (1983a): Social Organization Patterns of Several Feral Horse and Feral Ass Populations in Central Australia. *Z. Säugetierkunde* **48**, 124-126.
- (1983b): The Development of Social Behavior in Immature Males of a Feral Horse Population. Dissertation Universität Tübingen, W. Germany.
- IMANISHI (1950): Social Life of Semi-Wild Horses in Toimisaki III: Summary. *Physiology and Ecology* **4**, 28-29.
- JARMAN, P. J.; JARMAN, M. V. (1974): Impala Behaviour and its Relevance to Management. In: *The Behaviour of Ungulates and its Relation to Management*. Ed. by V. GEIST and F. WALTER. Morges, Switzerland.
- JOUBERT, E. (1972): Activity Patterns Shown by Mountain Zebra (*Equus zebra hartmannae*) in South West Africa with Reference to Climatic Factors. *Zool. Afr.* **7**, 309-331.
- KEIPER, R. (1976): Social Organization of Feral Ponies. *Proc. Pennsylvania Acad. Sc.* **50**, 69-70.
- KLINGEL, H. (1965): Notes on the Biology of the Plains Zebra, *Equus quagga boehmi*. *E. Afr. Wildl. J.* **3**, 86-88.
- (1969): Reproduction in the Plains Zebra, *E. burgchelli boehmi*: Behavior and ecological factors. *J. Reprod. Fert. Suppl.* **6**, 339-345.
- (1969): The Social Organization and Population Ecology of the Plains Zebra (*Equus quagga*). *Zool. Africana* **4**.
- (1972): Handbuch der Zoologie VIII, 10. Teil.
- (1974): A Comparison of the Social Behavior of the Equidae. In: *The Behavior of Ungulates and its Relation to Management*. Ed. by V. GEIST and W. WALTER. Morges, Switzerland.
- LE BOEUF, B. (1974): Male-male Competition and Reproductive Success in Elephant Seals'. *Amer. Zool.* **14**, 163-176.
- LENARZ, M. (1980): The Feral Horses on Cumberland Island, Georgia. pers. comm.
- LIN, D. (1983): Late Summer and Early Fall Grazing Habits of the Feral Horses on Bird Shoal-Carrot Island. Independent Study Project, Duke University Marine Lab.
- MARTIN, R. D. (1972): A Preliminary Field Study of the Lesser Mouse Lemur (*Microcebus murinus*). *Fortschritte der Verhaltensforschung* **9**, 43-89.
- McKNIGHT, T. (1958): The Feral Burrow in the United States: Distribution and Management. *J. Wildl. Managem.* **22**, 163-179.
- MILLER, R.; DENNISTON II, R. H. (1979): Interband Dominance in Feral Horses. *Z. Tierpsychol.* **51**, 41-47.
- MOEHLMAN, P. (1974): Behaviour and Ecology of Feral Asses (*E. asinus*). Ph. D. thesis, Univ. of Wisconsin.
- O'NEILL, T. (1980): pers. comm.
- POLLOCK, J. (1979): pers. comm.

- RHYMER, J. (1970): Social Behaviour of the Gower Ponies with Particular Reference to Social Organization. M. sc. Thesis; Univ. College Swansea.
- RUBENSTEIN, D. I. (1981): Behavioural Ecology of Island Feral Horses. *Equine vet. J.* 13, 27-34.
- SIEGEL, S. (1956): Nonparametric Statistics. McGraw-Hill.
- TRUMLER, E. (1959): Das Rossigkeitsgesicht und ähnliches Ausdrucksverhalten bei Einhufern. *Z. Tierpsychol.* 16, 478-488.
- TYLER, S. (1969): The Behaviour and Social Organization of the New Forest Ponies. Dissertation, University of Cambridge, Cambridge U.K. 1969, quoted from Waring (1983).
- (1972): The Behaviour and Social Organization of the New Forest Ponies. *Animal Behav. Monog.* 5, 85-196.
- VAN LAWICK-GOODALL, J. (1968): The Behaviour of Free-Living Chimpanzees in the Gombe Stream Reserve. *Anim. Behav. Monog.* 1, 161-311.
- VON GOLDSCHMIDT-ROTHSCHILD, B.; TSCHANZ, B. (1978): Soziale Organisation und Verhalten einer Jungtierherde beim Camargue-Pferd. *Z. Tierpsychol.* 46, 372-400.
- WARING, G. (1970): Primary Socialization of Foals (*E. caballus*). *Bull. Ecol. Soc. Amer.* 52, 45.
- WARING, G. (1972): Socialization and Behavioural Development of Newborn American Saddlebred Horses. Paper presented to Deutsche Veterinärmed. Gesellschaft, Freiburg, Br.
- (1983): *Horse Behavior*, Noyes Publications.
- WELLS, S.; VON GOLDSCHMIDT-ROTHSCHILD, B. (1979): Social Behaviour and Relationships in a Herd of Camargue Horses. *Z. Tierpsychol.* 49, 363-380.
- WELSH, (1973): The Life of Sable Island Wild Horses. *Canad. Nat. Fed.* Apr.-June 7-14.
- WILEY, H. (1980): Social Structure and Individual Ontogenies: Problems of Description, Mechanisms and Evolution. In: Perspectives in Ethology IV. Ed. by BATESON and KLOPPER. Plenum Press.
- WILLIAMS, M. (1974): Effect of Artificial Rearing on Social Behaviour of Foals. *Equine Vet. J.* 6, 17-18.
- WOODWARD, S. (1979): The Social System of Feral Asses (*E. asinus*). *Z. Tierpsychol.* 49, 304-316.
- ZEEB, K. (1958). Paarungsverhalten von Primitivpferden in Freigehegen. *Säugetierk. Mitt.* 6, 51-59.
- (1959): Die Unterlegenheitsgebärde des noch nicht ausgewachsenen Pferdes (*E. caballus*). *Z. Tierpsychol.* 16, 489-496.
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WISSENSCHAFTLICHE KURZMITTEILUNG

Der Cuvier-Schnabelwal (*Ziphius cavirostris*) im östlichen Mittelmeer

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Obwohl in einer sehr verstreuten Literatur für die östliche Mediterraneis 14 Arten von Walen (Cetacea) angegeben werden, liegt nur für ganz wenige mehr an Information vor als eine Aufzählung einiger Strandungen oder einzelner Belegstücke in öffentlichen Sammlungen. Für fast keine Art gibt es Untersuchungen über die Häufigkeit, Wanderungen, Fluktuationen oder weitere Einzelheiten der Biologie.

Viele Arten werden in Faunenlisten sogar nur genannt, ohne daß Belege nachgewiesen sind. Zu diesen zählte bis vor kurzem auch der Cuvier-Schnabelwal *Ziphius cavirostris* (Cuvier, 1823). Erst BAUER (1978) publizierte einen exakten Nachweis. MARCHESSAUX