Behaviour 112 (3-4) 1990, E.J. Brill, Leiden

INSTABILITY OF HAREMS OF FERAL HORSES IN RELATION TO SEASON AND PRESENCE OF SUBORDINATE STALLIONS

by

ELIZABETH FRANKE STEVENS[1)2)]
(Department of Biology, University of North Carolina,
Chapel Hill, N.C. 27514, U.S.A.)

(With 4 Figures)
(Acc. 16-V-1989)

Introduction

This paper examines the ecological and demographic factors that influence the female-defense mating system in a population of feral horses. A population of feral horses (*Equus caballus*) inhabiting sandy islands of the Rachel Carson Estuarine Sanctuary (RCES) conforms in general to the female-defense social structure (EMLEN & ORING, 1977) described for 4 species of equids (KLINGEL, 1974): *E. zebra*, *E. burchelli*, *E. przewalskii*, and *E. caballus*. The basic social unit is a band, consisting of the harem stallion and a harem of one to several females and their offspring.

Harem stability has a direct effect on a male's reproductive success. In this population, a stallion's reproductive success is positively related to the number of females in his harem (Fig. 1). Membership in a harem has been reported to last an individual's lifetime in several populations of harem-holding equid species (*Equus quagga*, KLINGEL, 1969a; *Equus zebra zebra*, KLINGEL, 1969b, 1979; PENZHORN, 1984; *Equus caballus*, DUNCAN *et al.*, 1984; TYLER, 1972). Even when a band's harem stallion has died, the harem has stayed together and been taken over as a unit by a new stallion (*Equus zebra zebra*, KLINGEL, 1979). In the RCES population, however, adult females changed harems during the winter and spring months preceding the breeding season each year.

[1)] Current address: Conservation and Research Dept., Zoo Atlanta, 800 Cherokee Ave., S.E., Atlanta, GA 30315, U.S.A.

[2)] I would like to thank Rolf HOFFMAN for beginning to study and to census this population in 1977. I am very grateful to Ted STEVENS and Andrea GROSSE for their long hours of assistance in the field. I owe very special thanks to R. Haven WILEY for hours of stimulating discussions which served to generate ideas and organize and focus my thoughts. Many thanks to Peter KLOPFER, Helmut MÜLLER, Devra KLEIMAN, and John SEIDENSTICKER for their constructive comments on the manuscript.

Studies of other feral horse populations have reported harem instability during winter and spring preceding the breeding season, but none has explored possible explanations for this seasonal difference in behaviour. Over a three-year period in the Great Basin, 50% of the mares that were four years old or older changed bands (BERGER, 1986). Sixty-one percent of the females in the Jicarilla Wild Horse Territory, New Mexico, changed bands (NELSON, 1978). In the Red Desert (MILLER, 1981) and in the Jicarillo Wild Horse Territory (NELSON, 1978), band changes occurred during the winter and early spring. In 1985 and 1986, 30% of the adult females on RCES (Table 1) changed harems (this figure does not include female juveniles leaving their natal bands).

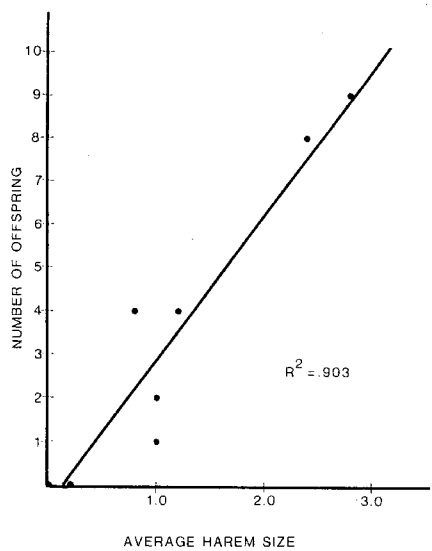

Fig. 1. Male reproductive success and harem size. Each point indicates one male's average harem size over the five-year period, 1981-1985, versus the number of offspring fathered by that male over the same five-year period ($Y = 3.37x - 0.46$, $R^2 = 0.903$, $p < 0.005$, $df = 6$). Only males of reproductive age (at least five years old) during the entire period, 1981-1985, were used in the analysis.

The seasonal differences in harem stability suggest that there are underlying ecological explanations for this behavior. For the RCES population the two most stressful seasons of the year are late winter, preceding the breeding season, and the breeding season from April through early July. During late winter the availability of fresh green vegetation is at its lowest (HAY & WELLS, 1988). The predominant species of forage, *Spartina alterniflora*, does not grow during winter, so that much

of the winter's forage consists of dead *Spartina alterniflora* and other dune grasses. Although food becomes more available during the breeding season (the biomass of *Spartina alterniflora* increases 5-10 fold; HAY & WELLS, 1988), stress is high while males are seeking copulations and females are bearing their offspring and lactating. Demands of foraging might influence the time budgets and spacing of band members and thus the stability of harems.

The composition of the bands and the social interactions within the bands could also affect the stability of harem membership. Half of the 12 bands present on the islands during the study period were "multi-male" bands, containing more than one stallion. Only one of these stallions succeeded in mating, the harem stallion. The multi-male bands contained from 1-3 other stallions, called subordinate stallions. A subordinate stallion is a permanent member of the band, clearly subordinate to the harem stallion, but not the offspring of the harem stallion or any of the females in the band. A subordinate stallion probably never copulates; in the over 100 observed mounting attempts, only one involved a subordinate stallion. This attempt was terminated when the harem stallion chased the subordinate stallion away from the female. Although not themselves mating with females, subordinate stallions might influence the chances females have to change bands.

The purpose of this paper is to examine harem stability in relation to seasonal differences in behavior and ecology and the social relationships between members of a band. Harem stability directly affects a male's reproductive success. A complete understanding of why harems are less stable during the winter and spring months preceding the breeding season requires consideration of behaviour outside the breeding season as well as during the breeding season (ROWELL, 1988). Specifically, I examine differences in the proportion of time devoted to grazing, spatial relationships between band members, and the frequency of social interactions, between two ecologically different seasons, summer and late winter. In addition, I examine demographic differences between stable and unstable bands to determine if harem size, age of the harem stallion, or the presence of subordinate stallions affected harem stability.

Study population and study site

The Rachel Carson Estuarine Sanctuary (RCES) is composed of four small islands of sand dunes and salt marsh totaling about 192 ha, located approximately 0.5 km off the coast of Beaufort, North Carolina, and 1.5 km from the barrier island, Shackleford Banks. The horse population is believed to have originated from a few individuals which immigrated to the island from nearby Shackleford Banks approximately 40 years ago.

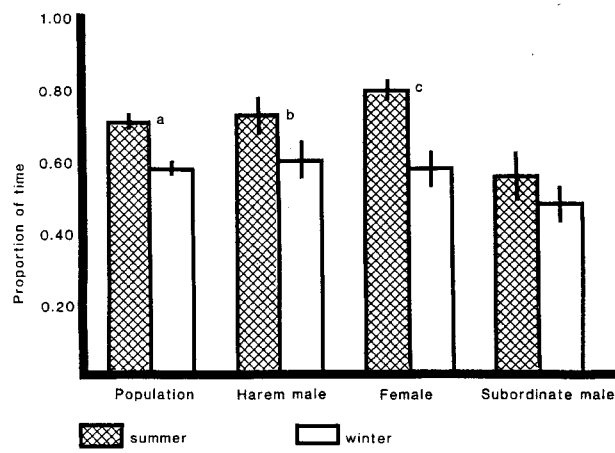

Fig. 2. Spacing between individuals. The average proportion of time spent within 10 m of another band member (mean proportion ± standard error) for the population as a whole, harem stallions, subordinate stallions, and females. [a] $p < 0.0005$, t-test (arcsin transformation, $t = 3.706$, $n_1 = 41$, $n_2 = 52$). [b] $p < 0.05$, Wilcoxon Matched Pairs Signed Ranks test ($N = 11$, $T = 12$). [c] $p < 0.005$, Wilcoxon Matched Pairs Signed Ranks test ($N = 21$, $T = 11.5$).

Until 1977 no accurate records of the population were kept. Since 1977, when only 25 horses were present (HOFFMAN, 1983), the number of individuals has increased steadily. During this study, from 1984-1986, the population increased in size from 44 to 68.

Individuals' distinguishing characteristics included body color, mane color, sex, facial markings, leg markings, scars, and the side of the neck on which the mane fell. I kept a file of photographs of all individuals throughout my study. My identifications correspond with those of HOFFMAN (1983), so that the ages and social roles of all individuals are known for each year since 1977.

The two principal species of forage are *Spartina alterniflora*, found in intertidal areas, and *Spartina patens*, found in the supratidal areas on the sand dunes. *Spartina alterniflora* is widely distributed in all intertidals areas and salt marshes, both above and below the mean tide level. Sources of fresh water are unevenly distributed across the islands and their abundance and supply vary with rainfall (FRANKE STEVENS, 1988). The bands are not territorial; all bands have been found in all areas of the study site.

Methods and materials

This study was conducted during the breeding season (April through July) 1985 and the prebreeding season (January through March) 1986. Behavioural observations of bands employed focal sampling (J. ALTMANN, 1974). Each band was observed for a total of 10-14 hours per season, evenly distributed over the daylight hours. The total number of focal-band hours for the two seasons was 235 hours.

During each focal-band hour the activity, nearest neighbour, and nearest-neighbor distance were recorded every five minutes for each individual in the focal band. All behavioural interactions involving members of the focal band were also recorded.

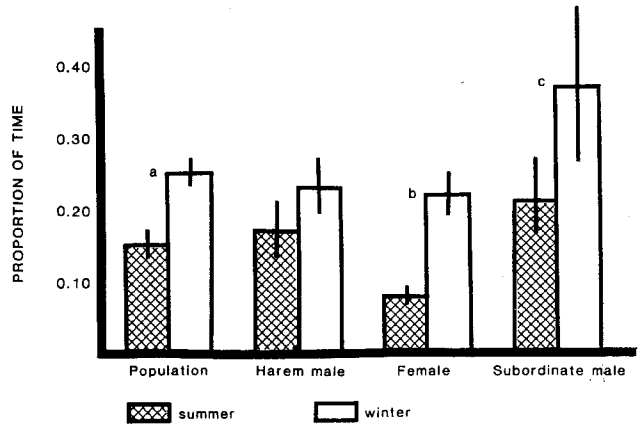

Fig. 3. Spacing between individuals. The average proportion of time spent greater than 20 m from any band member (mean ± standard error) for the population as a whole, harem stallions, subordinate stallions, and females. [a] $p < 0.001$, t-test (arcsin transformation, $t = -3.44$, $n_1 = 39$, $n_2 = 52$). [b] $p = 0.039$, Wilcoxon Matched Pairs Signed Ranks test ($N = 7$, $T = 3$). [c] $p < 0.05$, Wilcoxon Matched Pairs Signed Ranks test ($N = 21$, $T = 19$).

Results

Proportion of time spent grazing.

The horses spent significantly more time grazing during late winter when forage was poor. They grazed on average 71% (± 16%) of the daylight hours during the summer, and 86% (±8%) during the winter ($P < 0.0005$, t-test after arcsin transformation of proportions, $t = -5.386$, $n_1 = 41$, $n_2 = 52$).

Spacing between individuals.

An individual's location with respect to other band members affects the types of interactions that are likely to occur. I measured spacing in two ways: the proportion of time within 10 m of another band member and the proportion of time greater than 20 m from another band member. The former corresponds to a distance at which interactions are easily initiated, the latter to a distance at which interactions are unlikely. On average, harem stallions and females spent significantly more time within 10 m of another band member in summer than in winter (Fig. 2). Subordinate stallions also spent a slightly higher proportion of time within 10

m of other band members in summer than in winter, but the difference was not significant (Fig. 2).

Individuals overall spent on average 25% of their time greater than 20 m from another band member in winter but only 15% in summer (Fig. 3). This difference was statistically significant for subordinate stallions and females. Harem stallions, on the other hand, showed no significant difference between seasons in this measure (Fig. 3).

Nearest neighbors.

The proportion of time that males had one of their harem females as their nearest neighbors is an index of their access to females. Harem stallions had at least one of their harem females as a nearest neighbor on average 79% (Fig. 4) of the time in summer. This figure is significantly greater than in winter, when females were a nearest neighbor only 64% of the time (Fig. 4). In both seasons, harem stallions had at least one harem female as a nearest neighbor more often than did subordinate stallions (Fig. 4).

Behavioural interactions.

In general, the frequencies of behavioural interactions were lower in winter than in summer, both within bands and between bands (Table 1). The most common aggressive interactions were bites, kicks, and threats. A horse threatens another by laying its ears back on its neck and pointing its nose at its opponent. Aggression between females occurred approximately once every four hours, and there was no significant difference in the frequency of aggression between the two seasons. Aggressive interactions between males and females occurred equally as infrequently, with no significant difference between the breeding season and the prebreeding season (Table 1).

The two most frequently observed male-female behavioral interactions were driving and sniffing. Males sniffed females' noses and genitalia significantly more often during the breeding season than in the winter months (Table 1). Driving behavior by males usually occurred when a male was trying to make a female move in a particular direction. The typical driving posture of the male included a lowered neck with ears laid back and nose pointed toward the rear of the female(s). Driving behaviour was seldom observed in winter. Males drove females significantly more often during the breeding season than during the winter (Table 1).

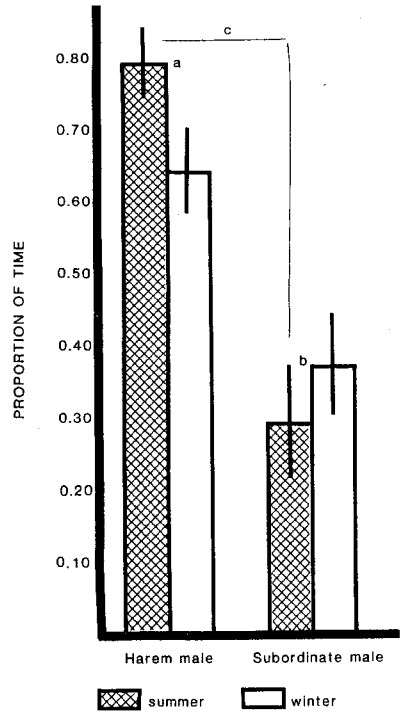

Fig. 4. The average proportion of time that a stallion's nearest neighbor was a female (mean ± standard error). [a] $p<0.001$, Mann-Whitney U test ($U = 1$, $n_1 = 7$, $n_2 = 11$). [b] $p<0.025$, Mann-Whitney U test ($U = 11.5$, $n_1 = 6$, $n_2 = 11$). [c] $p<0.025$, Wilcoxon Matched Pairs Signed Ranks test ($N = 11$, $T = 10$).

Interactions between bands occurred when two bands passed each other or whenever two or more bands grazed in close proximity to one another. Only stallions were involved. In single-male bands, it was always the harem stallion that interacted with the other band's stallion. In multi-male bands, the subordinate stallion participated in significantly more between-band interactions than did the harem stallion (paired t-test, $N = 6$, $t = 3.32$, $p<0.025$). The frequency of between-band interactions was significantly less in the prebreeding season than in the breeding season (Table 1).

Which females changed bands?

In 1985 and 1986, 10 females changed bands prior to the onset of the breeding season. Table 2 compares the characteristics of these females to those that did not change bands.

TABLE 1. Rates of behavioral interactions (bouts/hr)

	Summer		Winter
Aggression			
Female-female	0.24		0.29
Male-female	0.21		0.30
Driving frequency	3.3	*	0.91
Male sniff female	0.49	**	0.24
Between band interactions	0.88	***	0.48
Hours of observation	139		96

* $p < 0.005$, Wilcoxon Matched-Pairs Signed-Ranks test, $N = 12$, $T = 1$. ** $p < .05$, Wilcoxon Matched-Pairs Signed-Ranks test, $N = 10$, $T = 9.5$. *** $p < .01$, Wilcoxon Matched-Pairs Signed-Ranks test, $N = 12$, $T = 1$.

TABLE 2. Summary of characteristics of females that changed bands compared to females that did not change bands

	Changed bands mean ± s.d. (N)		Dit not change bands mean ± s.d. (N)
Average age			
1985	4.6 ± 2.1 (5)	NS	7.0 ± 2.9 (13)
1986	8.6 ± 2.5 (5)	NS	6.6 ± 3.0 (14)
Overall	6.6 ± 3.0 (10)	NS	6.8 ± 2.9 (27)
Average age of harem stallions			
1985	6.7 ± 5.8 (3)	*	10.5 ± 2.1 (6)
1986	10.0 ± 3.2 (4)	NS	9.5 ± 3.2 (8)
Overall	8.6 ± 2.9 (7)	NS	9.9 ± 2.7 (14)
Harem size before changes			
1985	2.3 ± 0.6 (3)	NS	2.2 ± 0.8 (6)
1986	2.3 ± 1.0 (4)	NS	1.5 ± 0.8 (8)
Overall	2.3 ± 0.8 (7)	NS	1.8 ± 0.8 (14)

* $p = .002$, Mann-Whitney U test, $U = 0$, $n_1 = 5$, $n_2 = 6$.

There were no significant differences between the ages of females changing bands and those not changing bands in either year or in both years combined (Table 2).

Although in 1985 harem stallions that lost females were significantly younger than harem stallions with stable harems, in 1986 there was no such difference. Combining both years, there was no significant difference between the ages of harem stallions with stable versus unstable harems (Table 2). There were also no significant differences in the sizes of the harems that females left and the sizes of stable harems (Table 2).

Females left single-male bands significantly more often than expected by chance (all 10 females left single-male bands; $\chi^2 = 7.24$, $df = 1$, $p < 0.01$). Since single-male bands appear to have unstable harems while multi-male bands do not, it is appropriate to compare the two types of bands to determine if there are any features that might explain this difference.

The average harem size of single-male bands was 2.2 in 1985 and 2.0 in 1986; for multi-bands the average harem size was 2.3 in 1985 and 1.5 in 1986. In neither year was the difference in harem size significant between single-male and multi-male bands. The average age of the harem stallion did not differ significantly between the two types of bands either. In 1985 the average age of harem stallions of single-male bands was 9.3 years, while harem stallions in multi-male bands were 9.7 years old. In 1986 the former averaged 9.0 years old and the latter 10.3 years old.

In winter the proportion of time spent within 10 meters of another band member or greater than 20 meters from another band member did not differ for females in single-male bands versus females in multi-male bands. In summer, however, females in multi-male bands spent a significantly greater proportion of time within 10 meters of another band member than did females in single-male bands. Also in the summer females in multi-male bands spent significantly less time greater than 20 meters from another band member than did females in single-male bands.

Although the frequency of driving behaviour by males during winter was greater for multi-male bands (1.17 ± 1.76 bouts/hr) than for single-male bands (0.60 ± 0.5 bouts/hr), this difference is not significant ($p = 0.469$, Mann-Whitney U test, $U = 17$, $n_1 = 6$, $n_2 = 6$). During summer the frequency of driving behavior was significant greater in multi-bands (3.77 ± 2.73 bouts/hr) than in single-male bands (2.67 ± 0.67; $p < 0.032$, Mann-Whitney U test, $U = 5.5$, $n_1 = 6$, $n_2 = 6$).

Discussion

In a female-defense mating system, a male's lifetime reproductive success depends on his ability to attract and retain females. For species in which males defend harems year-round, as in equids and a few primates like hamadryas baboons (*Papio hamadryas*) and patas monkeys (*Erythrocebus patas*), lifetime reproductive success of males depends upon the male's ability to keep females together during nonbreeding periods. This

problem does not arise in species in which males defend harems only during the breeding season, as in red deer (*Cervus elaphus*) (CLUTTON-BROCK *et al.*, 1982) and elephant seals (*Mirounga angustrostris*) (LE BOEUF, 1974).

The most obvious ecological difference between summer and winter is the lack of fresh growth of forage in the winter. The increased proportion of time spent feeding during the winter can be attributed to the low quality of forage. An increased proportion of time devoted to grazing in winter has also been reported for horse populations in the Camargue (DUNCAN, 1980), and on Assateague island (KEIPER *et al.*, 1980). These results are consistent with BERGER's (1986) finding that horses inhabiting poor habitats of the Great Basin spent a significantly greater proportion of time grazing than horses in habitats of high quality. KEIPER *et al.* (1980) and BERGER (1986) reported similar feeding times for day and night.

The poorer winter grazing also explains why band members are farther apart in winter than during the breeding season. Individuals must move around more to graze. The importance of the distribution of resources is now widely recognized to influence social organization. Where there are continuously renewing resources in high densities, animals can forage efficiently in large groups. On the other hand, if a resource is both slowly renewing and patchy in distribution, each patch supports only a few consumers (S. A. ALTMANN, 1974; GEIST, 1974; JARMAN, 1974; PULLIAM & CARACO, 1984; RUBENSTEIN, 1986). During winter, when the preferred forage, *Spartina alterniflora*, is not growing, the horses of RCES respond by increasing their distances from other band members. In other large herbivores as well, group sizes or spacing of group members changes with foraging conditions. Group sizes of female greater kudu (*Tragelaphus strepsiceros*) decrease during the dry season when vegetation is sparsely distributed (SPINAGE, 1986). In patas monkey (*Erythrocebus patas*) harems, adult males were farther from other group members during the dry season preceding the mating season than at any other time of the year (HALL, 1965). Even small groups of bovids fragment if individuals must move at different speeds or move far apart to meet their feeding requirements (JARMAN, 1974).

The combination of additional time devoted to grazing and increased distances between individuals contributes to the lower frequency of behavioural interactions in the winter. Most noticeably absent is the driving behaviour of males. Males drive females 3-4 times more often during the breeding season than during winter. Driving is the principal

behaviour used by the male to keep his females together. Its absence, combined with the greater distances between individuals and the increased focus on grazing, permit some females to wander from their harems.

Another factor that might influence the movement of females between bands is aggression between females, which might be expected to increase during ecologically stressful periods when females in the same harem compete for the available food. Increased aggression toward young females by band members has been proposed (KLINGEL, 1974; PENZHORN, 1984) to cause them to disperse from their natal bands during the months preceding and during the breeding season. My data, however, show that increased aggression does not explain why adult females change bands. The frequency of aggression between adult females of the RCES population is low, and it does not increase during late winter.

Other factors that might influence movement of females between bands include the age of the harem male, the size of the harem, and the presence of a subordinate stallion. One might expect that younger, less experienced males would find it more difficult to keep a harem together. However, in the two years of this study, there was no such effect of age: harem stallions of all ages lost females from their harems. Nor was it the case that females of larger harems were more likely to leave.

The effect of a subordinate stallion, on the other hand, was clear. The single characteristic in common for all of the 10 females that changed bands was that they left single-male bands. MILLER (1981) also reported this relationship for the Red Desert horses. Even though I could measure no behavioural differences between single-male bands and multi-male bands in behaviour during the winter, presumably the presence of an additional male on the periphery of a band contributes to harem stability. The absence of this extra male in single-male bands could explain why females in these bands wander off more easily. Subordinate males in multi-male bands in this population derive a benefit from their participation in bands: they stand a chance to inherit the harem eventually.

This study has thus shown that the harsh ecological conditions of winter make it more difficult for males to maintain their harems. As individuals have to move farther from other band members to forage during winter, it becomes more difficult for males to keep their females together. This explanation might also apply to other populations of horses in which foraging is difficult during winter and spring months preceeding the breeding season (MILLER, 1981; NELSON, 1978). Under such conditions, bands with more than one male have a greater chance of keeping their harems together than do single-male bands.

Summary

Male horses (*Equus caballus*) defend harems of females (bands) year-round and throughout their lifetimes. A male's lifetime reproductive success depends upon the number of females in his harem. Although harems have previously been reported as remaining stable over many years, during the two years of this study 30% of the adult females in an island population of feral horses changed harems during late winter. The seasonal differences in harem stability resulted from seasonal differences in the abundance and distribution of food. The spacing between band members was greater and the frequency of social interactions between them was lower in winter than in summer. In addition, the amount of time devoted to grazing increased in winter. These differences are attributed to the lower availability of suitable vegetation duirng winter. Harem stability did not depend on the age of females, the size of the harem, nor the age of the harem stallion, but did depend on the presence of subordinate stallions attached to the band. All of the females that changed bands left single-male bands; multi-male bands were stable throughout the study.

References

ALTMANN, J. (1974). Observational study of behaviour: sampling methods. — Behaviour 49, p. 227-267.

ALTMANN, S. A. (1974). Baboons, space, time, and energy. — Amer. Zool. 14 (1), p. 221-248.

BERGER, J. (1986). Wild horses of the Great Basin. — Univ. of Chicago Press, Chicago.

CLUTTON-BROCK, T. H., GUINNESS, F. E. & ALBON, S. D. (1982). Red deer: Behavior and ecology of two sexes. — Univ. of Chicago Press, Chicago.

DUNCAN, P., FEH, C., GLEIZE, J. C., MALKAS, P. & SCOTT, A. M. (1984). Reduction of inbreeding in a natural herd of horses. — Anim. Behav. 32, p. 520-527.

EMLEN, S. T. & ORING, L. W. (1977). Ecology, sexual selection and the evolution of mating systems. — Science 197, p. 215-223.

FRANKE STEVENS, E. (1988). Contests between bands of feral horses for access to fresh water: the resident wins. — Anim. Behav. 36, p. 1051-1053.

GEIST, V. (1974). On the relationship of social evolution and ecology in ungulates. — Amer. Zool. 14, p. 205-220.

HALL, K. R. L. (1965). Behaviour and ecology of the wild Paras monkey, *Erythrocebus patas*, in Uganda. — J. Zool. 148, p. 15-87.

HAY, M. E. & WELLS, J. T. (1988). Effects of feral horses on the production, distribution, abundance, and stability of saltmarsh plants: Rachel Carson component of the North Carolina National Estuarine Research Reserve. — Final Report for NOAA Grant #NA87AA-D-CZ023 to the N.C. Dept of Natural Resources and Community Development.

HOFFMAN, R. (1983). The development of social behaviour in immature males of a feral horse population, *Equus caballus*. — Ph.D. Thesis, Universität Tübingen.

JARMAN, P. J. (1974). The social organization of antelope in relation to their ecology. — Behaviour 58, p. 215-267.

KEIPER, R. R., Moss, M. B. & ZERVANOS, S. M. (1980). Daily and seasonal patterns off feral ponies on Assateague Island. — Conference on Scientific Research in the National parks (2nd.) Vol. 8, p. 369-381.

KLINGEL, H. (1969a). The social organisation and population ecology of the plains zebra, *Equus quagga*. — Zoologica Africana 4, p. 249-263.

—— (1969b). Dauerhafte Sozialverbande beim Bergzebra. — Z. Tierpsychol. 26, p. 965-966.

—— (1974). A comparison of the social behaviour of the Equidae. — In: The behaviour

of ungulates and its relation to management (V. GEIST & F. WALTHER, eds). IUCN New Series Pub. No. 24, p. 124-132.

(1979). A comparison of the social organization of the Equids. — Symposium on the Ecology and Behavior of wild and feral equids, Univ. of Wyoming, Laramie, Sept. 6-8, 1979, p. 23-28.

LEBOEUF, B. J. (1974). Male-male competition and reproductive success in elephant seals. — Amer. Zool. 14, p. 163-176.

MILLER, R. (1981). Male aggression, dominance, and breeding behavior in Red Desert feral horses. — Z. Tierpsychol. 57, p. 340-351.

NELSON, K. J. (1978). On the question of male-limited population growth in feral horses, *Equus caballus*. — Masters Thesis, New Mexico State University, Las Cruces, New Mexico.

PENZHORN, B. L. (1984). A long-term study of social organisation and behaviour of Cape Mountain zebras *Equus zebra zebra*. — Z. Tierpsychol. 64, p. 97-146.

PULLIAM, R. & CARACO, T. (1984). Living in groups: is there an optimal group size? — In: Behavioural ecology, An evolutionary approach (J. R. KREBS & N. B. DAVIES, eds). Sinauer Associates Inc., Sunderland, Massachusetts, p. 122-147.

ROWELL, T. E. (1988). Beyond the one-male group. — Behaviour 104, p. 189-201.

RUBENSTEIN, D. I. (1986). Ecology and sociality in horses and zebras. — In: Ecological aspects of social evolution, birds and mammals (D. I. RUBENSTEIN & R. W. WRANGHAM, eds). Princeton U. Press, Princeton, N.J., p. 282-302.

SPINAGE, C. A. (1986). The natural history of antelopes. — Facts on File Publications, New York.

TYLER, S. (1972). The behavior and social organization of the New Forest ponies. — Anim. Behav. Mon. 5, p. 87-196.

Zusammenfassung

Männliche Wildpferde (*Equus caballus*) verteidigen ihr ganzes Leben lang, und während des ganzen Jahres, einen aus mehreren Weibchen bestehenden Harem. Der Gesamtfortpflanzungserfolg eines Hengstes ist von der Anzahl der Stuten in seinem Harem abhängig. Obwohl bisher immer berichtet wurde, dass sich die Haremszusammensetzung über mehrere Jahre nicht ändert, wechselten während der zwei Jahre dieser Untersuchung 30% der erwachsenen Weibchen die Haremszugehörigkeit gegen Ende des Winters. Die saisonalen Unterschiede in der Haremsstabilität waren eine Folge von saisonalen Schwankungen der Nahrungsfülle und Nahrungsverteilung. Der räumliche Abstand zwischen Gruppenmitgliedern war im Winter grösser als im Sommer, während die Häufigkeit der sozialen Interaktionen innerhalb der Gruppen im Winter geringer war. Ausserdem nahm die Gesamtzeit die die Pferde mit Weiden verbrachten im Winter zu. Diese Unterschiede werden auf die geringere Verfübarkeit von geeigneter Vegetation im Winter zurückgeführt. Die Stabilität eines Harems war weder vom Alter der Stuten, noch von der Haremsgrösse oder von Alter des Haremhengstes abhängig, sondern hing allein von der Anzahl der einer Gruppe zugehörigen untergeordneten Hengste ab. Alle Stuten die die Gruppe wechselten verliessen Gruppen mit nur einem Hengst; Gruppen mit mehreren Hengsten hatten während der gesamten Beobachtungszeit eine stabile Zusammensetzung.