

## REDUCTION OF INBREEDING IN A NATURAL HERD OF HORSES

BY P. DUNCAN,\* C. FEH\*, J. C. GLEIZE\*, P. MALKAS\* &amp; A. M. SCOTT†

\**Station Biologique de la Tour du Valat, Le Sambuc, F-13200 Arles, France*

and

†*Equine Research Station, Snailwell Road, Newmarket, Suffolk, U.K.*

**Abstract.** A genetically-isolated herd of 14 Camargue horses left unmanaged for 6 years produced 58 living foals and developed a social system similar to that of wild horses. Paternity of the foals was determined by blood-typing. Inbreeding coefficients were calculated and were lower than expected on the hypothesis that mating was random with respect to relatedness. The horses showed reduced levels of sexual behaviour with members of their entourage as juveniles—mother, herd stallion and maternal siblings.

Inbreeding is used in artificial selection of domestic animals in order to fix desired heritable traits rapidly (Lasley 1972). In the Quarterhorses of the King Ranch, for instance, the average Inbreeding Coefficient is 0.049 (Evans et al. 1977).

Close inbreeding, however, is known to have deleterious effects on vigour and fecundity in many species (see Clutton-Brock & Harvey 1976; Greenwood 1980) including horses (Bouman & Bos 1979). Indeed it has been argued that one of the main functions of juvenile dispersal is the achievement of outcrossing in mammals and birds (Greenwood 1980; Dobson 1982).

Feral horses and plains and mountain zebra live in small closed-membership bands (Klingel 1975). The stallions practise mate-defence polygyny and the adults may remain together for several years. The young born into these bands are therefore surrounded by close kin (parents and siblings); generally both sexes transfer out of their natal band at puberty (Klingel 1975; Penzhorn 1979). It has been argued that the function of this dispersal is to avoid inbreeding (Feist & McCullough 1976). In fact there are other plausible explanations for such transfers: young males could disperse to avoid reproductive competition with their fathers, and individuals of both sexes might leave to avoid feeding competition with adult group members.

Such hypotheses, which are not mutually exclusive, are difficult to test by observing stable social systems. Because young horses generally move away at puberty, only exceptionally will close kin have the opportunity to mate; similarly competition between adults and post-pubertal young will not often be observed.

We have been fortunate in being able to observe an unstable system in which a domestic

herd of horses developed a feral-type social system under close surveillance. Kinship was known, and the herd contained three different blood-lines, so each horse was exposed to both close kin and unrelated individuals.

In this paper we test the hypothesis that the horses avoided close kin in their sexual and social behaviour.

## Materials and Methods

## The Horses

The horses were all of the Camargue breed, which has been established in the Rhône Delta for hundreds, perhaps thousands of years (Berriot 1969). While there is no evidence that these horses have ever lived as wild or feral animals, they have been managed in large herds on extensive pastures, with little care until recent years. Mortality rates of the order of 15% per year, though exceptional, still occur (personal observation) and it can be assumed that selective pressures for behavioural and morphological characters adapted to the animals' environment have been significant in historical times.

The horses are small (135–145 cm at the shoulder) and reach adult weight (430 kg) at about 7 years of age (personal observation). They are hardy and for the period of this study were given no supplementary fodder or veterinary treatment.

The herd used for this study has existed on the Tour du Valat estate in the eastern Camargue at least since the 1930s. No females were ever added to it. An adult stallion was run with the herd for breeding each year from April to about September, until 1973.

The study herd of 14 animals consisted initially of a 5-year-old stallion, six mares aged 4–19 years, three 2-year-olds (two males and one

female) and four yearlings (two males, two females). Each was serially referenced by a letter-number combination, e.g. D1, where the letter identified the year of birth ( $D=1969$ ). They were released into an area of 300 ha, later increased to 335 ha, in December 1973 and were left without management until September 1979.

During the first 3 years (1974–1976) the herd's social structure was loose and typical of the domestic herds (Wells & von Goldschmidt-Rothschild 1979). There was a clear linear dominance hierarchy with few reversals between horses aged over 2 years. Spatial relations were not rigid, but 'matriarchal families' were clearly distinguishable, for male and female offspring generally maintained close relations with their mothers until their third year. The sex-ratio of breeding animals was female biased, rising from 33% of males to 47% of males. The nine post-pubertal males (over 18 months) all mated during this period.

Over the next 2 years (1977–1978), the number of potential breeders increased to 44 (sex-ratio = 45% males) and the social structure became more complex, with the appearance of seven closed-membership bands whose composition and interactions resembled closely those of the non-territorial zebra and mustang populations which have so far been studied.

Foals were born in each month from November to August, but not in the other months, so for this analysis foals born in November and December were grouped with those of the following spring. Sixty-two foals were born during the five years 1975–1979, of which four died at birth. The numbers of horses present at the beginning of each foaling season and the numbers of foals born are shown in Table I.

#### Field Observations and their Analysis

From April 1974 the herd was visited on at least 20 days per month for a variety of studies

**Table I.** The Numbers of Horses Present at the Beginning of each Foaling Season (November), and the Numbers of Foals which Survived Long Enough to Furnish Blood Samples

Year	Horses	Foals
1974	14	6
1975	20	7
1976	26	9
1977	34	9
1978	43	13
1979	56	20

(social behaviour, time-budgeting, use of habitat, etc.). During these visits, which were of variable frequency and duration, records were made of the nearest neighbour of each horse at intervals of at least half an hour. The data for 1979 are used in this paper: these were collected on a tape recorder in the field, then grouped by season and analysed using single linkage cluster analysis (Morgan et al. 1976). There were always seven reasonably well-defined clusters and for the annual summary, which allowed us to establish the composition of the social groups, we constructed a matrix of the number of seasons (out of five) in which each horse was observed in the same cluster as each other one (see Wells & von Goldschmidt-Rothschild 1979).

A mating was said to occur when a horse, with penis extended, mounted a female. Matings were recorded throughout the study, both during systematic observations and on an ad libitum basis whenever they were seen.

#### Genetic Relationships

For the period before the study (1948–1973) a herd log was maintained by the farm manager (F. Rensch, R. Lambert personal communication). The mother of each foal was recorded, as was the presumed father, the stallion present in the herd 11 months before the foal was born. Only a single stallion was present at any one time.

For the study period the father was determined by the paternity exclusion method. A male was considered a potential sire from the time it was 18 months old and it was assumed that the foals were sired by males belonging to the study herd only, there being no evidence to the contrary.

The blood of each horse was sampled in September 1979 and the blood-type determined by standard techniques (Scott 1978). Twenty-eight loci were studied.

For nine foals it was not possible to exclude all but one stallion. In these cases the likelihood method was used: if at a given locus the foal in question has the genotype PQ and the mother QQ, then potential fathers with the genotype PP are deemed to be twice as likely to have sired the foal as potential fathers with heterozygous genotypes of the type PQ (Edwards 1972; Foltz and Hoogland 1981). Such exclusions were backed up by field data on matings.

The relatedness of each pair of horses (e.g. I8, K8), measured as the Additive Relationship ( $a$ ), was calculated as described by Evans et al. (1977):

$$a_{I8 \times K8} = \frac{1}{2} (a_{I8 \times C1} + a_{I8 \times D1})$$

where K8 is the younger horse and C1, D1 its parents.

Thus if I8, K8 are full siblings then

$$\begin{aligned} a_{I8 \times C1} &= \frac{1}{2} \text{ (C1 is mother of I8)} \\ a_{I8 \times D1} &= \frac{1}{2} \text{ (D1 is father of I8)} \\ a_{I8 \times K8} &= \frac{1}{2} \end{aligned}$$

The Inbreeding Coefficient ( $f$ ) of each horse (e.g. K8) was calculated as:  $f_{K8} = \frac{1}{2}(a_{C1 \times D1})$ .

#### Expected Levels of Inbreeding

In order to test the hypothesis that the horses avoided breeding with close kin, we required an estimate of the probability of a conception between each female-male pair.

The post-pubertal mares conceived annually with few exceptions (see below); the stallions on the other hand, differed greatly in reproductive success (0-6 foals per year). Reproductive success was closely correlated with age (see below), and varied from year to year. We therefore weighted each potential sire each year by the proportion of foals he sired in that year, to obtain the probability that he mated with a given mare. As an example, the expected numbers of father-daughter conceptions ( $N_{exp}$ ) were calculated by

$$N_{exp} = \sum_{i=1}^n (m_i \cdot p_i) \quad (1)$$

where

$m$  = the number of conceiving daughters of the  $i$ th stallion;

$p$  = the proportion of foals of that year sired by the  $i$ th stallion;

$n$  = the number of potential sires (over 18 months).

The expected level of inbreeding ( $f_{exp}$ ) for each foal was calculated by

$$f_{exp} = \sum_{i=1}^n (f_i \cdot p_i) \quad (2)$$

where  $f_i$  = the Inbreeding Coefficient of the foal had its mother been impregnated by the  $i$ th stallion.

## Results

### Determination of Paternity

As a first step the blood types of the horses sired before the study began were examined in the light of their genetic relationships deduced from the herd log. All but one were consistent with the presumed relationships; the erroneous one was corrected.

For the 58 surviving foals sired during the study, all except one potential sire could be excluded in 49 cases (85%). The father of the remaining nine foals was taken as the most probable sire on the basis of a likelihood analysis (Table II). In each case (except N7) this was the only one of the possible fathers which had been seen to mate the mother one gestation length earlier (11 months). In the case of N7, there was no record of her mother having been mated by either of the possible fathers in the previous year, 1978, but the genetically more likely (H1) had been seen in a pre-copulation display with her in 1978 and had mated her earlier in the study. The other possible sire, H4, had never been observed to mate this mare: H1 was therefore assumed to be the father. The parents of each horse are given in the Appendix.

Twenty-one mares bred successfully, usually producing a foal each year after puberty (mean  $\pm$  SD =  $0.954 \pm 0.21$  foals per year). Of 14 potential sires, six had no offspring (mean  $\pm$  SD =  $1.49 \pm 2.04$  foals). The success of the eight sires varied considerably, and was closely correlated with their age (Table III:  $r_s = 0.98$ ,  $P < 0.01$ ).

### Genetic Relatedness and Inbreeding

The Additive Relationship ( $a$ ) between each pair of horses, and the Inbreeding Coefficient ( $f$ )

Table II. Foals with More than One Possible Father, with the Results of Likelihood Analyses and Relevant Field Observations

Foal	Possible fathers	Most probable father	Matings observed previous year, by possible fathers	Remarks	Assumed father
L1	G4, H4, I3	G4 or H4	H4 $\times$ 7	G4 in different band	H4
M7	D1, J1	D1	D1 $\times$ 3	J1 in different band	D1
M8	H1, H4	H1	H1 $\times$ 4		H1
M9	G4, H4	G4	G4 $\times$ 1	H4 in different band	G4
M13	G4, I6	G4	G4 $\times$ 2	I6 in different band	G4
N1	H1, H4	H1	H1 $\times$ 8	H4 in different band	H1
N7	H1, H4	H1		H1 showed pre-mating behaviour	H1
N15	H1, H4	H1	H1 $\times$ 3	H4 in different band	H1
N17	H1, H4	H1	H1 $\times$ 8	H4 in different band	H1

of each were calculated as described above. The resulting matrix ( $76 \times 76$ ) is available on request.

The values of  $f$  varied between 0 and 0.344; their distribution followed a poisson law; the median value was 0.031.

For each generation of foals the median value of the observed  $f$  was lower than the expected, as calculated by equation 2 (Fig. 1). The difference was significant for the foals sired during the early years, 1974-1976, with a domestic-type social structure (Kolmogorov-Smirnov two-sample test  $K_D = 11$ ,  $N = 25$ ,  $P = 0.025$ ) as well as in the later years, 1977 and 1978, with a feral-type social structure (1977:  $K_D = 7$ ,  $N = 13$ ,  $P = 0.05$ ; 1978:  $K_D = 9$ ,  $N = 20$ ,  $P < 0.05$ ). Quantitatively, the reduction in the median level of inbreeding was considerable, the observed value never exceeding half of the expected.

#### Origin of the Reduction in Inbreeding

The reduction in the level of inbreeding in the herd could be accounted for if there had been a general tendency among the females to mate with the least-related males.

The average Additive Relationship of each sire with all the reproductive mares, weighted by the number of foals they produced is given in Table III together with the number of foals per sire. There was a positive, though non-significant, correlation between the two variables ( $r_s = 0.557$ ,  $N = 8$ ), so the origin of the reduction in consanguinity was sought at the level of individual male-female relationships, the most consanguineous being mother-son, father-daughter and sibling-sibling.

**Mother-son (M-S) pairings.** The matings observed are summarized in Table IV. None of the stallions was observed to mate with its mother;

Table III. Age, Total Number of Offspring and Relatedness to Mares\* of the Effective Sires During the Years 1974-1978

Sires	Age (years in 1979)	Offspring	Relatedness to mares
D1	10	18	0.103
G4	7	19	0.242
H1	6	7	0.163
H4	6	4	0.166
I3	5	4	0.130
I4	5	3	0.131
I5	5	2	0.145
I6	5	1	0.128

\*The average relatedness of each sire to the mares, weighted by the number of foals they produced, is given.

the most successful, G4, mated with every mare except his mother. The four oldest stallions (D4 to H4) were involved in the great majority of matings: avoidance of M-S pairings is clearly shown by these horses with respect to the eight oldest mares born before the study began (9 to H2). The only empty cells in this partial matrix are M-S pairs (G4-9, H1-E1, H4-9; the mother of D1 was not in the herd). The number of matings per pair is significantly lower in M-S pairs ( $\bar{X} = 0$ ,  $N = 3$ ) than in other pairs ( $\bar{X} = 11.8$  matings;  $t = 14.4$ ,  $P < 0.001$ ; comparison of the means of small samples, log transformation).

No foals were born to M-S pairs, though only 2.51 were expected (equation 1 all years). Mother-son pairings were therefore avoided.

**Father-daughter (F-D) pairings.** Matings were observed between similar proportions of F-D pairs (0.45,  $N = 11$ , see Table IV) and other pairs (0.50,  $N = 157$ ;  $\chi^2 = 0.0$ ,  $df = 1$ ,  $P > 0.5$ ). Two foals resulted from F-D matings (G4-J3; G4-K5), compared with an expected number of 3.14 (equation 1, all years). There was, therefore, no evidence for any reduction of sexual activity between such pairs.

The 13 young females, I1 to L3, were all born in the herd of which D1 was the dominant stallion. D1 mated less with these mares (median = 0 per heat,  $N = 13$ ; Table IV) than with the older mares which had not been born into his herd (median = 2.25 per heat,  $N = 8$ ;  $P = 0.005$ , median test with Fisher's exact probability test). D1 sired foals with each of the older mares, but

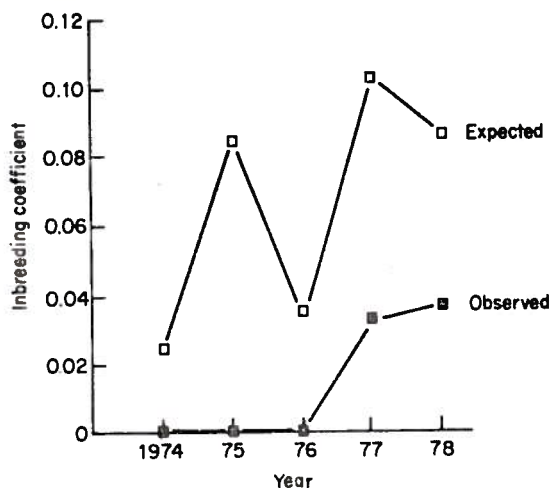


Fig. 1. Expected and observed values of the Inbreeding Coefficient of foals sired in the years 1974-1978.

Table IV. Matings Observed Between Breeding Mares and the Stallions of the Study Herd, 1974-1979

Mares	Stallions								Number of heats
	D1	G4	H1	H4	I3	I4	I5	I6	
9	14	*	6	*					6
5	13	13	2	1		*	1		6
7	15	38§	33	8§	*				6
C1	10	3	9	4			8	5	6
D2	9	3	12	2		§		3	6
E1	16	18	*	14	§		*		6
G3	13	23§	6	6				*	6
H2	25	12	7§	6§		†	7		6
I1	3	24	11	6	§	28§	6§	2§	5
I2	4	2	3§	2§	8				4
I7	1†	4†	4	†		6			3
I8	1†	13	10	11					3
J3	1	1†	1†	2		11	†	2	3
J4	†	6	1		1	†	2		3
J5	†	3					1	†	3
J6	†	6§		1†	7				2
K2	†	2			3		11		3
K5		3†				†			2
K7		7†		1	1		3		2
L1		2		†	§	5	1		2
L3	†	2	§	4			§		2

\*Mother-son pairs.

†Father-daughter pairs.

‡Siblings which at some stage were part of the same matriarchal family.

§Other siblings.

with none of the younger mares ( $P < 0.005$ , Fisher's exact probability test).

There was therefore no evidence for avoidance of father-daughter matings, but there was a reduction of sexual activity between fillies and the stallion of their natal band.

**Sibling pairings.** Mating was observed in a similar proportion of sibling (half and full) pairs as in non-sibling pairs (0.54, 0.51;  $N = 26, 142$ ; see Table IV). Seven foals were born to siblings, compared with 9.32 expected (equation 1, all years). There was, therefore, no evidence for avoidance of sexual relations between siblings in general.

Nine of the sibling pairs had experience of their relationship as they had been contemporary members of the same matriarchal family. The frequency of matings between these siblings (median = 0,  $N = 9$ ) was lower than between other siblings (median = 2 per heat;  $N = 17$ ;  $P = 0.05$ , median test with Fisher's exact probability). In one of the rare cases of a known-sibling mating the observer reported that the female made considerable efforts to escape. No foals were born to known sibling pairs, but only 1.6 were expected; see equation 1.

There was therefore some evidence for reduced sexual activity between siblings which had associated simultaneously with their mother, but none between siblings in general.

#### Social Structure and Genetic Relatedness

The original herd divided into seven bands in the years 1977-1978. These bands contained one or two stallions and two to nine reproductive mares (Fig. 2). No further transfers of adults have occurred between these bands (up to December 1982).

The average Additive Relationship of each stallion with the mares of its own, and of the other bands is given in Table IV. Most of the stallions were less related to mares of their own bands than to the mares in other bands, and the difference was significant ( $N = 9$ ;  $T = 4$ ;  $P < 0.05$ ; Wilcoxon matched-pairs, signed-ranks test). There was therefore evidence that, when forming permanent social bonds, the horses preferred unrelated or distantly-related individuals to close kin.

None of the pairs mother-son, filly-stallion-of-natal-band or contemporary maternal siblings occurred among the adult horses of these bands

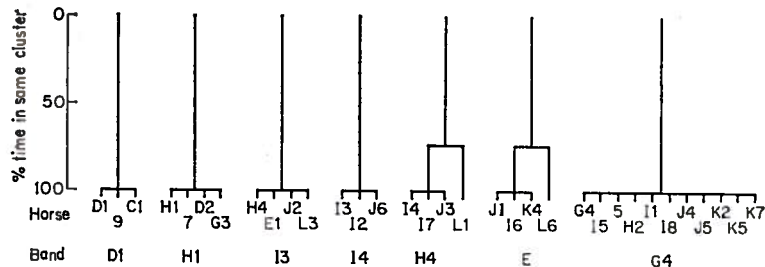


Fig. 2. Single linkage cluster analysis of the proximity relations of the post-pubertal horses in 1979.

(see Fig. 1 and Table V). There were, however, one pair of non-contemporary maternal siblings (I6-L6), one of paternal siblings (J1-K4) and two father-daughter pairs (G4-K5, G4-K7).

### Discussion

The application of the blood-typing method for the determination of paternity was aided in this study by the fact that we had a small number of stallions which were reasonably polymorphic at the 28 loci we examined.

This method provided unequivocal results for the great majority of foals (85%); paternity of the remaining foals was determined by likelihood analysis, the conclusions of which were consistent with field observations of sexual behaviour.

As in many species, reproductive success varied less between females (0-1 foal per year) than between males (0-6 foals sired per year). The success of a male over the 5 years was closely related to his age, which in turn was correlated with his dominance status in the early years ( $r_s = 0.99$ , calculated from data in Wells & von Goldschmidt-Rothschild 1979).

Under these semi-natural conditions the levels of inbreeding remained low (median inbreeding coefficient  $< 0.04$  each year). The expected level, calculated by weighting each stallion according to his reproductive success, was significantly higher, both during the early years and after the division of the herd.

This reduction of inbreeding did not result from any general tendency of the mares to mate with less-related stallions for there was a positive, though non-significant, correlation between the stallions' reproductive success and their average relatedness to the mares.

The most consanguineous offspring result from parent-offspring and sibling matings. Both occurred and resulted in offspring in this herd. The horses did not, therefore, recognize and avoid all close kin. There was, however, an

avoidance of mother-son pairings. There were also reduced levels of sexual behaviour between fillies and the stallion of their natal band, who would normally be their father, and between maternal siblings which had been contemporary members of their mother's matriarchal family. These horses therefore showed reduced levels of sexual activity with the members of their immediate social entourage when juvenile, not with close kin per se. These results do not provide evidence for genetically-based recognition of close kin such as has been found in some species (e.g. pigtail macaques, Wu et al. 1980), but they do imply that the mechanisms which led to the reduction of inbreeding were based on experience. This kind of sexual imprinting has been found in a number of other mammals (e.g. Hoogland 1982) and in birds (e.g. Bateson 1978) and is considered to be a primary mechanism of incest avoidance in animal societies (Harvey et al. 1980).

The development of long-lasting social bonds between adult males and females in the year 1977-1978 followed the pattern of sexual relationship in the early years. There was no general avoidance of close kin, but mother-son, filly-stallion-of-natal-band and contemporary mater-

Table V. The Stallions' Average Additive Relationship With Mares in Their Own and in Other Bands

Stallions	Average additive relationship	
	Own mares	Other mares
1	0	0.20
G4	0.20	0.27
I5	0.09	0.15
H1	0.18	0.15
H4	0.07	0.20
I3	0.07	0.12
I4	0.06	0.13
I6	0.14	0.11
J1	0.18	0.20
median	0.09	0.15

nal siblings did not occur in the same bands. As a consequence most stallions had relatively-unrelated mares in their bands.

These horses showed behaviour patterns which led to the reduction of inbreeding without the complex social organization which is found in wild herds. It is therefore probable that the dispersal of young horses which, in mature societies, generally occurs at puberty (e.g. Penzhorn 1979) is a consequence of the reduced levels of sexual activity between the young horses and their immediate entourage.

### Acknowledgments

This study was funded by the Foundation Tour du Valat and the Equine Research Laboratory of the Animal Health Trust (A. M. Scott). We are most grateful to all our colleagues who helped to collect the behavioural data and to catch the horses for the blood sampling. Pamela Moncur and Melanie Barclay carried out the tedious calculations for the matrix of Additive Relationships. The text was considerably improved as a result of the comments of two anonymous referees.

### Appendix. Parentage of Horses in the Tour du Valat Herd, 1974-1979

Horse	Sex	Mother	Father	Year of birth	Horse	Sex	Mother	Father	Year of birth
9	F	X1	X2	1955	L2	M	D2	H4	1977
5	F	X1	X3	1961	L3	F	E1	D1	1977
7	F	9	X4	1964	L4	M	I2	I3	1977
C1	F	X5 <sup>†</sup>	X6	1968	L5	M	5	D1	1977
D1	M	X7	X8	1969	L6	F	G3	H4	1977
D2	F	5	X9	1969	L7	M	H2	D1	1977
E1	F	7	X9	1970	L8	M	9	D1	1977
G2	M	X5	X9	1972	M1	F	I1	G4	1978
				(1976)	M2	F	I8	H1	1978
G3	F	X10	X9	1976	M3	M	E1	D1	1978
G4	M	9	X9	1976	M4*	F	J3	G4	1978
H1	M	E1	X11	1973	M5	M	J4	G4	1978
H2	F	5	X11	1973	M6	M	J5	I3	1978
H3	F	7	X11	1973	M7	F	5	D1	1978
				(1975)	M8	M	I7	H1	1978
H4	M	9	X11	1975	M9	F	H2	G4	1978
I1	F	C1	X12	1974	M10†	M	I2	H1	1978
I2	F	D2	X11	1974	M11	M	G3	D1	1978
I3	M	7	X12	1974	M12†	M	J6	G4	1978
I4	M	5	X12	1974	M13	M	K2	G4	1978
I5	M	E1	X12	1974	M14	F	C1	D1	1978
I6	M	G3	X12	1974	N1	M	D2	H1	1979
I7	F	9	D1	1974	N2	F	E1	H4	1979
I8	F	C1	D1	1974	N3*	M	K5	G4	1979
J1	M	7	D1	1975	N4	M	I1	G4	1979
J2	F	D2	D1	1975	N5	F	J3	I4	1979
J3	F	E1	G4	1975	N6	M	I8	G4	1979
J4	F	5	D1	1975	N7	F	9	H1	1979
J5	F	G3	D1	1975	N8	M	5	G4	1979
J6	F	9	D1	1975	N9	F	K7	I3	1979
J7	M	C1	G4	1975	N10	M	J4	G4	1979
K1†	M	7	G4	1976	N11	M	J5	G4	1979
K2	F	D2	D1	1976	N12	M	I7	I4	1979
K3	M	E1	G4	1976	N13	M	I2	I3	1979
K4	F	H2	D1	1976	N14	F	H2	I5	1979
K5	F	5	G4	1976	N15	F	G3	H1	1979
K6†	M	G3	G4	1976	N16	F	L1	I4	1979
K7	F	I1	G4	1976	N17	M	7	H1	1979
K8	M	C1	D1	1976	N18	F	L3	I6	1979
L1†	F	7	H4	1977	N19	F	K2	I5	1979

Those horses which were not part of the study herd are indicated by a code name consisting of X+number.

Year of death, where appropriate, is given in parentheses.

Type of mating:

\*Father-daughter.

†Siblings not from same matriarchal family.

## REFERENCES

- Bateson, P. 1978. Sexual imprinting and optimal outbreeding. *Nature, Lond.*, **273**, 659-660.
- Berriot, C. 1969. Le cheval de Camargue. D.Vet. thesis, Ecole Nationale Vétérinaire, Lyon, France.
- Bouman, J. G. & Bos, H. 1979. Two symptoms of inbreeding depression in Przewalski horses living in captivity. In: *Genetics and Hereditary Diseases of the Przewalski Horse* (Ed. by I. Bouman & J. T. Bouman), pp. 111-117. Rotterdam: Foundation for the Przewalski Horse.
- Clutton-Brock, T. H. & Harvey, P. H. 1976. Evolutionary rules and primate societies. In: *Growing Points in Ethology* (Ed. by P. P. G. Bateson & R. A. Hinde), pp. 195-237. Cambridge: Cambridge University Press.
- Dobson, F. A. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Anim. Behav.*, **30**, 1183-1192.
- Edwards, A. F. W. 1972. *Likelihood*. Cambridge: Cambridge University Press.
- Evans, J. W., Borton, A., Hintz, H. F. & van Vleck, L. D. 1977. *The Horse*. San Francisco: W. H. Freeman.
- Feist, J. D. & McCullough, D. R. 1976. Behaviour patterns and communication in feral horses. *Z. Tierpsychol.*, **41**, 337-371.
- Foltz, D. W. & Hoogland, J. L. 1981. Analysis of the mating system in the black-tailed prairie dog (*Cynomys indolicianus*) by likelihood of paternity. *J. Mammal.*, **62**, 706-711.
- Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.*, **28**, 1140-1162.
- Harvey, P. H., Baker, M. C., Bateson, P., Bischof, N., Emlen, S. T., Holldobler, B., Kramer, B., Linsenmair, K. E., Markl, H., Marler, P., Menzel, E. W., Micheuer, C. D., Milinski, M. & Trillmich, F. 1980. Mechanisms of kin-correlated behaviour. Group report. In: *Evolution of Social Behaviour: Hypotheses and Empirical Tests* (Ed. by H. Markl), pp. 183-202. Weinheim: Verlag Chemie.
- Hoogland, J. L. 1982. Prairie dogs avoid extreme inbreeding. *Science, N.Y.*, **215**, 1639-1641.
- Klingel, H. 1975. Social organisation and reproduction in equids. *J. Reprod. Fert., Suppl.*, **23**, 7-11.
- Lasley, J. F. 1972. *Genetics of Livestock Improvement*. Englewood Cliffs, New Jersey: Prentice Hall.
- Morgan, B. J. T., Simpson, M. J. A., Hanby, J. P. & Hall-Craggs, J. 1976. Theory and application of cluster analysis. *Behaviour*, **56**, 1-43.
- Penzhorn, B. L. 1979. Social organisation of the Cape Mountain zebra *Equus z. zebra* in the Mountain Zebra National Park. *Koedoe*, **22**, 115-156.
- Scott, A. M. 1978. Immunogenetic analysis as a means of identification in horses. In: *Proceedings of the IVth International Congress on Equine Infectious Diseases* (Ed. by J. J. Bryans & H. Gerber), pp. 259-268. Princeton, New Jersey: Veterinary Publications.
- Wells, S. M. & von Goldschmidt-Rothschild, B. 1979. Social behaviour and relationships in a herd of Camargue horses. *Z. Tierpsychol.*, **4**, 363-380.
- Wu, H. M. H., Holmes, W. G., Medina, S. R. & Sackett, G. P. 1980. Kin preference in infant *Macaca nemestrina*. *Nature, Lond.*, **285**, 225-227.

(Received 10 May 1982; revised 7 June 1983;  
MS. number: 2252)