

Consequences of natal dispersal in female horses

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Abstract. Social, genetic and reproductive consequences of natal dispersal were investigated in female horses, *Equus caballus*, living in a herd with a natural social structure. Dispersal did not as a rule reduce the level of competition the young mares faced: they did not selectively join groups with fewer resident females than the groups they left, and they did not attain higher ranks; there was also no tendency for females to disperse to groups with the fewest resident females, and they suffered more aggression from the mares in their new groups than in their natal groups. These results therefore do not support the hypothesis that a function of natal dispersal is to reduce intra-sexual competition. The young mares nevertheless dispersed non-randomly, generally joining harems with one stallion and at least two subadult females; and they preferred to move to groups with familiar females but no familiar males. As a result, most were closely related to some females of their new groups, but distantly related or unrelated to the male(s). Since after dispersal the young mares bred only with a male of their new groups, inbreeding coefficients of most (85%) of their offspring were lower than from matings between half siblings. These results are consistent with the hypothesis that a function of natal dispersal is to avoid close inbreeding. Dispersal did not appear to involve reproductive costs: the young mares suffered no delay in age at first reproduction, and the survival rates of their first foals tended to be higher if the females had emigrated, although not significantly so.

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Investigating the functions of natal dispersal requires estimates of the fitness costs and benefits involved (e.g. Bengtsson 1978; Shields 1987; Johnson & Gaines 1990). Two major contrasting functional hypotheses have been proposed for natal dispersal in mammals, both implying that individuals gain fitness benefits through emigration: the avoidance of close inbreeding, and the reduction of intra-sexual competition for resources or mates (for reviews see Greenwood 1980; Moore & Ali 1984; Dobson & Jones 1985; Pusey 1987).

Most studies have focused primarily on the proximate causes of emigration, or on the patterns of immigration, and the data needed to evaluate the costs and benefits of dispersal are rarely available in natural populations of mammals, particularly in group-living species. This is because the fate of dispersing individuals is

difficult to monitor (Johnson & Gaines 1990) and immigrants are usually of unknown origin (but see Pusey & Packer 1987a; Smith 1992 for reviews on primates; Pusey & Packer 1987b for lions, *Panthera leo*; Creel & Waser 1994 for dwarf mongooses, *Helogale parvula*). There is also little known about the factors influencing the choice of groups to join, the genetic relatedness between immigrant and resident individuals and the levels of inbreeding of dispersers' offspring. This is especially true for species where females emigrate. In some species dispersal has fitness costs: dispersing individuals may have lower survival rates (e.g. Johnson & Gaines 1990; Isbell et al. 1993; Larsen & Boutin 1994), and/or in the case of females lower reproductive success caused by a delay in first reproduction or reduced survival of their progeny (e.g. Waser & Jones 1983; Pusey & Packer 1987b; Crockett & Pope 1993; Wiggett & Boag 1993). The assessment of such costs is obviously of crucial importance in understanding the functions of dispersal.

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In this paper we examine the consequences of natal dispersal for young females in a closely monitored herd of horses, *Equus caballus*, with a natural social structure in which, as in other populations of harem-forming equids, both sexes disperse (Feh 1990; Monard 1992). The advantages of this herd were: (1) it has been minimally managed and has developed a natural social system similar to that of wild and feral populations; (2) during our study the horses were habituated to observers, individually known and closely monitored (including the use of biochemical methods for paternity determination), so that their life histories were known in detail, including those of 40 young females; and (3) we could collect quantitative data on the social and reproductive behaviour of 12 young females during dispersal (Monard 1992).

Here we identify some of the social, genetic and reproductive consequences of transferring to other groups in the light of the two explanatory hypotheses. The inbreeding avoidance hypothesis postulates that dispersal evolved as a means of avoiding the loss of fitness which results from close inbreeding in normally outbred populations, owing to an increase in homozygosity, that is, inbreeding depression (e.g. Charlesworth & Charlesworth 1987). In mammals, evidence for inbreeding depression, including increased juvenile mortality, lowered fecundity and decreased longevity, has been documented in captive populations (e.g. Ralls et al. 1988; Laikre & Ryman 1991), and possibly in natural populations (Packer 1979; Pusey & Packer 1987b), where inbreeding depression may also cause increased vulnerability to pathogens (O'Brien et al. 1985). In feral and wild populations of equids, levels of inbreeding are unknown, but deleterious effects of inbreeding have been found in captive plains zebras, *Equus burchelli* (Ralls et al. 1979, 1988) and Przewalski's horses, *E. ferus przewalskii* (Bouman & Bos 1979; Ballou 1994), while the conclusions are equivocal in domestic horses (reviewed in Bouman & Bos 1979; Berger 1986).

Intra-sexual competition in female horses concerns access to resources (food, water, shelter, etc.), and perhaps to mates. We do not have direct measures of access to resources, but competition is expressed by a female displacing another (e.g. from a feeding site) with or without overt aggression (threats, bites, etc.). Females in horse societies develop dominance hierarchies, generally

linear (e.g. Rutberg & Greenberg 1990), which govern access to resources. In this herd, high-ranking females had diets of higher quality, and faster growing daughters that bred earlier in some circumstances (Duncan 1992, pp. 91, 166). Here, as in other studies (e.g. Watts 1985; Rutberg 1990), we use data on the frequency of aggression and on the rank of a female as indicators of the degree of competition she faced.

First we examine the social factors influencing the probability of joining particular groups and describe the process of integration into the new group. If the intra-sexual competition hypothesis is correct, we should expect that one or more of these predictions is confirmed: (1) young females transfer to groups with fewer females than their natal groups; they might also join groups with the fewest females; (2) they experience less aggression from mares in their new groups than in their natal groups; (3) they attain higher ranks in their new groups. The inbreeding avoidance hypothesis would be supported if young females transfer to groups with no familiar males, which are normally close relatives (brothers or half-brothers). We then examine the genetic effects of dispersal: the inbreeding avoidance hypothesis predicts that the progeny of the dispersing females should have inbreeding coefficients lower than from a mating with a half-brother. Using data on growth of the foals, we test for inbreeding depression. Finally, the fact that some females first reproduced before dispersing (Monard et al., in press) enabled us to evaluate some of the reproductive costs of dispersal. Dispersing females might breed later and have offspring with lower survival rates.

METHODS

Study Herd

We studied a herd of Camargue horses, established in December 1973 on the Tour du Valat estate in the southeast of the Camargue, France. The population rose from 14 in 1973 to nearly 100 animals in 1981; herd size was then maintained at 50–60 until 1987.

During the first 4 years (1974–1977), the horses' social structure changed from a 'domestic' type (Wells & von Goldschmidt-Rothschild 1979) to a near-natural one similar to that found in feral horses, and plains and mountain zebras, *Equus zebra* (Klingel 1974), with harems and bachelor groups.

All individuals were known from body characteristics (general shape, coat colour, etc.) or brands, and were serially referenced by a letter–number combination where the letter indicates the year of birth (e.g. I=1974). From September 1979 the herd was rounded up at least twice a year, in spring and autumn, for weighing, blood sampling and removals. Body condition was recorded monthly from October 1978, using a condition index (see Henneke et al. 1983) with six categories from 1 (excellent) to 6 (emaciated; Duncan 1992, page 154). We estimated weight and body condition for particular dates by interpolation. Mother's rank was known from the long-term monitoring data (see Duncan 1992, page 248), and individuals were allocated to social groups by cluster analysis of records of nearest neighbours (see Wells & von Goldschmidt-Rothschild 1979). The study area and management of the herd have been described fully in previous papers (see Monard et al., in press).

Subjects

Our subjects were the 40 females born between 1974 and 1985 that dispersed from their natal groups to other harems. The pattern, proximate causes and timing of dispersal have been described in detail elsewhere (Monard et al., in press). Data on four other females of these cohorts, which were removed before dispersal, were also used for the analyses of the level of inbreeding and the survival of their offspring.

Life History Data

The following life history data were available for males and females born between 1974 and 1985: the identity of the mother and father, birth date, the natal group, the group to which a few of the young mares moved with their mothers before dispersing themselves (18%; Monard et al., in press) and the composition of these groups, date of dispersal, the breeding group and its composition, the composition of the other groups at the time of dispersal, birth date of all offspring (for a few females birth dates of offspring born in the year after removal were not known), their survival and the identity of the fathers of those born up to 1986 (except for the foals that died before a blood sample was taken).

Since observations were made on most days, the dates of birth and dispersal were usually known

exactly, and the errors were never more than ± 2 days. A female was considered to have dispersed to her breeding group when she associated only with members of this group.

The fathers of the animals were determined by paternity exclusion based on blood-typing; where more than one stallion could have been the father of a foal the likelihood method was used, backed up by field observations of matings (see Duncan et al. 1984).

Genetic Relatedness and Inbreeding

The genetic relatedness between each immigrant female (e.g. Q7) and resident stallions and mares of her new (breeding) group (e.g. I4), measured as the additive relationship (a), was calculated as described by Evans et al. (1977):

$$a_{Q7 \times I4} = 0.5(a_{I4 \times K5} + a_{I4 \times I5})$$

where Q7 is the younger horse and K5, I5 its parents. We refer to close relatives as parents and offspring, full siblings and half siblings, that is, individuals with a equal to 0.50, 0.25, or more if they shared common ancestors; and to distant relatives as individuals with $a < 0.125$, the value for full cousins in an outbred population.

The inbreeding coefficients (f) of the offspring of females born between 1974 and 1985 were calculated as a half of the additive relationship between the female and the foal's sire. The f values for the offspring of close relatives are therefore greater than or equal to 0.125; those of distant relatives are less than 0.0625.

We could not evaluate the level of inbreeding depression on the fitness traits (juvenile survival and fecundity) commonly used because of the special circumstances of this study. We therefore tested the effects of inbreeding on growth during the most difficult period for young horses nutritionally, the first winter, by calculating their weight change between autumn and spring.

Behavioural Observations on Focal Females

Of the 40 subjects, eight were among the 12 young females studied in detail from weaning (or 1.5 years of age) to dispersal (Monard et al., in press). These eight were born to different mothers in five harems and were studied between March 1984 and September 1986 (range=4–11 months, for a total of 439 h), during the process of

integration into their new groups. They comprised four females of the 1982 cohort and two females of each of the 1983 and 1984 cohorts. They all transferred before breeding, directly from their natal groups to other harems, at between 20 and 35 months of age. Several (born in different groups) immigrated into the same breeding groups but not simultaneously (Q8 and Q9; Q10 and R9; R6, S13 and S15; at 1–12-month intervals). Q10 was the first female of a new harem, to which R9 transferred a year later. Q10 was removed 2 weeks after the arrival of R9; she therefore features in some analyses for R9, but not in those covering longer periods.

The females were observed between the beginning of winter and the end of summer. Each was observed using focal animal sampling (Altmann 1974), 1 h per observation day, on 10 days per month; there were at most 4 days between consecutive 1-h sessions. Observations were distributed equally between dawn and dusk, and were carried out on foot as the horses could be watched from distances of as little as 2 m without disturbance. We recorded two types of data.

(1) Social interactions: all social interactions initiated or received by the focal female were recorded, with the identity of the interacting horses. Interactions were grouped for analysis as affiliative behaviour (approaches, followings, friendly contacts and groomings), aggression, submission, sexual behaviour and herding behaviour. Herding behaviour has been observed only in adult males; it involves lowering the neck and head with the ears retracted while pushing or driving females in a given direction (Berger 1986). Definitions for the other behaviour patterns are given in Monard (1992).

(2) Proximities: the first nearest neighbour of each focal female (defined as the closest horse to the female's head) was recorded four times per day, twice in the mornings and twice in the afternoons, with 1 h between, on 20 days per observation month, using instantaneous sampling (Altmann 1974); i.e. 80 observations/female/month.

We used agonistic data concerning 22 other dispersing females within their breeding groups, collected as part of the long-term project, for analyses of dominance/subordination (see below).

Matings were recorded both during systematic observations and on an ad libitum basis whenever they were seen; data were also available from the

long-term monitoring for females of the 1974–1985 cohorts.

Analyses

The horses of each sex were grouped into three age classes for the analyses: foals (birth to 12 months), subadults (12–48 months for males, or the birth of their first foal for females) and adults. 'Resident females' of a group includes adults and subadults that had immigrated into the group (excluding, therefore, daughters of group members). This distinction is necessary for the analyses of competition because newly immigrant subadult females ranked below resident females, subadults as well as adults, but always outranked the daughters that had not yet dispersed (see Results). Some females (18%) moved out of their natal groups with their mothers before themselves dispersing: 'maternal group' is used to denote the groups from which these females dispersed, as well as the (natal) groups from which the other young females emigrated.

To examine the process of integration into the new group, we studied changes over time in the affiliative relationships of the females that transferred between 1984 and 1986 by defining their preferred partners for proximities, affiliative interactions given and received, for 2-month periods (involving, on average, 160 proximity observations and 20 h of focal observations for interactions). The frequency of each horse as first nearest neighbour of the focal female, or as an interaction partner, was compared with that expected on the basis of a binomial distribution. The null hypothesis was that all the horses had the same probability of being first nearest neighbour (or partner for interactions); horses whose frequencies were significantly higher than expected were considered preferred partners.

We determined the dominance status of the females that dispersed between 1984 and 1986 after immigration, with respect to each member of their breeding groups. Within each dyad, the horse that gave significantly more aggressive interactions leading to a submissive response from the recipient was considered to be the dominant; the binomial test was used to evaluate the significance of differences (Soffié & Zayan 1978). The number of effective aggressive interactions given and received by each female is presented in Monard (1992, Appendix 6). For the females that dispersed

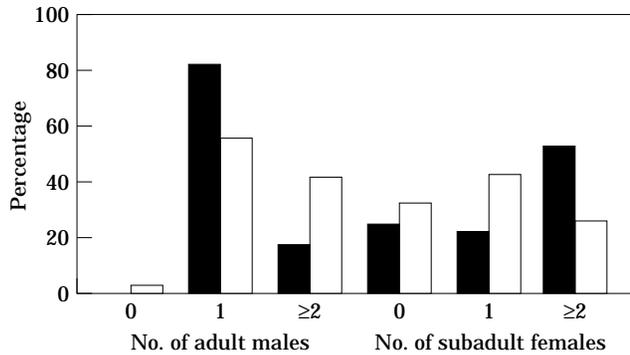


Figure 1. Percentages of adult males and subadult females in the groups to which young females transferred (■), and in the other groups (□). $N=40$ females, 1974–1985 cohorts.

in other years, we determined their dominance status within their new group after immigration with respect to adult and subadult females of this group using Schein & Fohrman's method (1955; see Wells & von Goldschmidt-Rothschild 1979), since agonistic data were too sparse for the binomial test. We estimated the rank of each horse by arranging individuals in an order so that each one received aggressive interactions from the smallest number of individuals below it.

To test whether the presence of familiar individuals influenced the choice of the breeding group, we compared the number of young females joining groups with, versus without, familiar individuals with the numbers expected had they dispersed randomly to the groups available at the time of dispersal. The sample sizes were small because many dispersing females had no choice: for some, born in the early years, there were familiar individuals in all the groups, and for others the reverse was true.

All statistical tests were two-tailed.

RESULTS

The Choice of the New Group

Group size and composition

Most females (67%, $N=21$) transferred to groups smaller than their maternal groups (Wilcoxon matched-pairs signed-ranks test: $T=34$, $N=19$, $P<0.05$; 19 other individuals had no choice since their maternal groups were larger than all other groups, and were excluded from this analysis): 76% joined groups containing fewer

offspring than their maternal groups ($T=2.5$, $N=17$, $P<0.01$). In contrast, there was no significant difference in the number of resident females: eight young females (38%) joined groups with one to three more resident females while nine (43%) joined groups with one to four fewer ($T=76$, $N=17$, ns), and for four there was no change. In addition, the 40 dispersing females showed no tendency to transfer to groups containing the fewest resident females: the median number of females in the groups to which they dispersed was two, in the other groups available it was one.

Immigration into a particular group was affected by the number of subadult females (i.e. including daughters of group members and immigrants); more of the groups that females joined had at least two subadult females (maximum number=5) compared with the other groups present at the time of transfer (Fig. 1; $G=11.12$, $df=2$, $P<0.01$, $N=40$ females, 297 group-females). In contrast, the number of adult females, subadult males, or foals, did not influence significantly the choice of the new group ($G=5.17$, 2.60, 0.25, respectively; $df=2$, ns, $N=40$ females, 297 group-females for all three age-sex classes).

The majority of young females (71% of 21) came from and dispersed to groups containing only one immigrant male; five others joined groups with one or two more males than the group they left. They transferred significantly more often than expected to groups with only one adult male, compared with groups with more than one male (Fig. 1; $G=9.27$, $df=1$, $P<0.01$, $N=40$ females, 297 group-females).

Finally, there was some evidence that attraction to one particular male (or group) influenced the

process of immigration. Of the females that transferred between 1984 and 1986, six of seven joined the group of the male whose sexual approaches they had been observed to accept prior to dispersal.

Presence of familiar individuals from the maternal group

Of 11 dispersing females that had familiar females outside their maternal groups, significantly more (seven, 64%) joined groups with one (six cases) or two (one case) familiar females (median percentage of groups with familiar females=12.5%; binomial test: $P<0.001$); these familiar females were 0–1 year older than the dispersers. None of the 11 dispersing females that had the choice joined groups containing familiar males, although this did not differ significantly from expected (median proportion of groups with familiar males=11%; binomial test: NS). The presence of familiar females (and perhaps males) therefore influenced the choice of the breeding group. The familiar individuals (females and males) were mostly close relatives so we were not able to determine whether relatedness played a separate role.

Integration into the New Group

Affiliative relationships

For the eight focal females we compared the frequency of each horse in the herd as first nearest neighbour with that expected on the basis of the binomial distribution, for each 2-month period; the same analysis was done for affiliative interactions given and received. After immigration most, or all, of the members of the focal female's new group were generally selected over the horses of the other groups. Only two females had horses from outside their breeding groups in this set; all of these were members of their natal groups: for one, a paternal half-brother in the period just after immigration; for the other, several group members during all the observation periods (the natal and breeding groups of this female associated closely after she transferred; unpublished data).

A further analysis, using the same method, was then performed to identify preferred partners within this selected group; the results for all females and periods are detailed in Monard (1992, Table XXV). There were never more than two

preferred partners for proximities and for affiliative interactions; they were always members of the new group right from the moment of immigration, and their ages and sexes varied according to group composition. The preferred partners of the six females that transferred to established harems were usually subadults of either sex for proximities and for affiliative interactions given and received (74%, 89% and 78% of cases, respectively), rarely adult females (26%, 5.5%, 5%), foals (0%, 0%, 17%) or the adult stallion (0%, 5.5%, 0%). In the period just after immigration all females attached themselves to one particular subadult female, either a resident female (four cases, one being a familiar paternal half-sister) or a daughter of group members (two cases). This subadult female was their preferred partner for affiliative interactions given and, with one exception, for proximities; in three cases this subadult female was also a preferred partner for affiliative interactions received. Two of the six immigrant females later maintained preferential affiliative relationships with this subadult female; the others switched to another subadult.

In contrast, the two females whose breeding groups contained only males (an adult stallion and a subadult in the two cases) had no preferred partner in the period just after immigration. During the next (and last observation) period, the adult stallion was the preferred partner of both females (for proximities and affiliative interactions, and for affiliative interactions, respectively).

We conclude that the young females rapidly integrated into their new groups. The links with members of the natal groups were generally broken immediately; and the young females formed close bonds with a subadult female, familiar or otherwise, when these were present in the new groups. The swiftness of this change is striking because all the animals normally lived in close proximity, the distance between adjacent groups usually ranging from 20 to 50 m in winter, and from 1 to 20 m in summer.

The role of the stallion of the new group

The integrity of horse breeding groups is maintained partly by herding behaviour shown by the adult stallions (e.g. Berger 1986), and there is evidence that in the Camargue herd the group stallion in some cases played a role in the

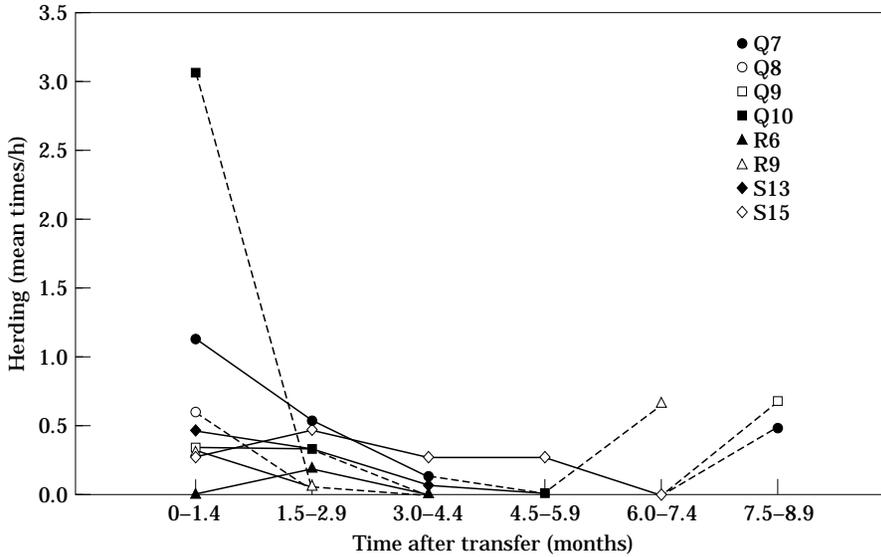


Figure 2. Changes over time in the frequency (over 15 h of observation) of eight focal females being herded by the adult stallion of their new groups. Q10 was the first female of a new harem.

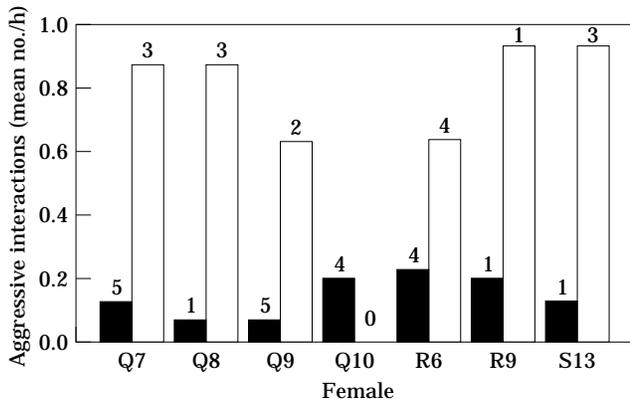


Figure 3. Frequency of aggressive interactions received by seven focal females from the median resident mare in their natal groups (■) and in their new groups (□) during periods of 1.5 months (over 15 h of observation) just before and after dispersal. Numbers above the bars are the number of resident mares in the group.

integration of young females into their new groups. Four out of the eight focal females were herded more often in the first period after immigration than in the subsequent ones (Fig. 2): this was very clear in the case of Q10 which was the first female in a new harem. However, being herded by the stallion appears not to be a necessary part of the process since in the four other cases there was no such trend; R6 was never observed being herded in the first period.

Dominance status in the new group

The focal females suffered significantly more aggression from resident females in their new groups than in their natal groups before transfer (Fig. 3; comparison of the number of aggressive interactions received from the median mare in the natal versus the breeding group; Wilcoxon matched-pairs signed-ranks test: $T=1$, $N=7$, $P<0.05$).

Table I. Dominance rank of young females in the year following immigration into their new group with respect to resident females of this group

Immigrant female	Rank†						
	1	2	3	4	5	6	7
1974–1976 cohorts							
I1*	H2	I1	J4‡				
I7	I7	J3‡					
K2	H2	I1	J4	J5‡	K2		
I8	H2‡	I1	J4‡	J5‡	I8§	K5‡	K2‡
K5	H2	I1	J4	J5‡	I8	K5	K2‡
1982–1984 cohorts							
Q7	I7	J3	Q7	Q3‡			
Q9	P20	O21	Q9				
Q8	P20	O21	Q9	Q8			
R9	Q10	R9					
S15	O2	P9	S15				
S13	O2	P9	S15	S13			
R6	O2	P9	S15	S13	R6		

*The cohort is shown by the letter (H=1973, . . . , S=1984).

†1=highest-ranking resident female of the immigrant female's group. Bold typeface indicates the immigrant female.

‡Female from the maternal group of the immigrant female, which was familiar and the daughter of a mare subordinate to the immigrant female's mother.

§I8 arrived in her breeding group at the same time as K5.

The dominance relations of immigrant females ($N=22$) with adult and subadult females of their new groups were clear. Immigrant females always outranked subadult females that were daughters of group members, irrespective of differences in age (the subadult females were 0–2 years younger), or the rank of the subadult females' mothers. Among the resident females the order of arrival was the prime determinant of rank, with newly immigrant females occupying the bottom rank. They were immediately subordinate to the adult females of their new groups, as well as the subadults that immigrated before them, irrespective of differences in age (the subadult females were 2 years older to 1 year younger; Table I). The only exceptions were females that transferred to groups with females from their maternal groups, which were both familiar and daughters of mares subordinate to their own mothers. Five out of six of these outranked such females, which had dispersed shortly before them (0–1 year before), and were the lowest ranking resident females in their new groups. These five females occupied the penultimate rank immediately after their integration, and in some cases even came to outrank other familiar females in later years.

In contrast, no clear dominance relations could be detected with the adult stallions, subadult males and foals, as agonistic interactions were very rare and often bi-directional. Overt competition for mates among resident females in a group was rare: only on one occasion in the focal observations was a female seen to interpose herself between the stallion and a subsequent immigrant during courtship.

Genetic Consequences of Natal Dispersal

Genetic relatedness with individuals of the new group

The additive relationship (a) of immigrant females with the resident females of their new groups ranged from 0 to 0.594; the median value (0.188) is intermediate between second and third-degree relatives (half siblings and cousins). Most females (59%, 20 of 34) joined groups with at least one closely related female (second or first-degree relative: $a \geq 0.25$); 13 (38%) joined groups with at least one female for which $0.125 \leq a < 0.250$; and only one was related less than in the third degree to all the mares of her breeding group.

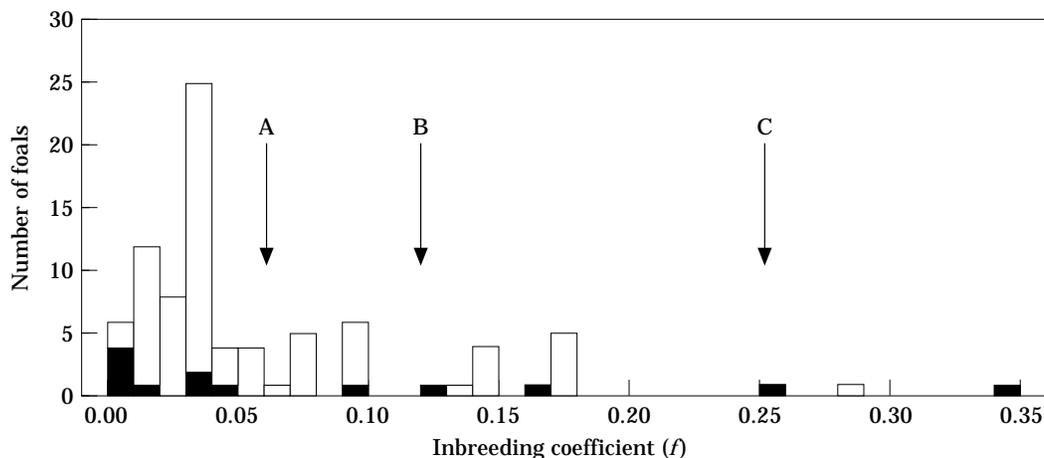


Figure 4. Frequency distribution of the inbreeding coefficients of the females' progeny ($N=86$ foals, born to 25 different females of the 1974–1985 cohorts). ■: Foals conceived before natal dispersal, □: foals conceived after natal dispersal. Inbreeding coefficients resulting from matings between cousins (A), half siblings (B) and full siblings or father–daughter (C).

Immigrant females were less closely related to the stallions than to the resident mares of their new groups (comparison of the additive relationship with the median mare versus the median stallion; Wilcoxon matched-pairs signed-ranks test: $z = -2.48$, $N=34$, $P < 0.05$). Their additive relationship with the stallion(s) had a similar range (0–0.563), but the median value (0.117) was lower. Only 12 (30%) joined groups with one or more closely related males ($a \geq 0.25$); for the majority of these females (8/12), these closely related males were not familiar individuals from their maternal groups; the remaining four females dispersed in the early years when there were no groups without familiar individuals.

Inbreeding levels of progeny

After dispersal young females were never seen to visit other groups when in oestrus, and were observed to mate almost exclusively with one particular adult stallion of their new groups: only three of 171 observed matings (2%; $N=32$ females) involved males from outside their breeding groups; and when the breeding groups contained several males (including adults and subadults; $N=17$ females), only three of 109 matings involved a subordinate male.

Paternity of the females' progeny was consistent with field observations of matings. No surviving

offspring that were conceived after female dispersal ($N=73$ foals, produced by 20 different mothers) were sired by males from outside their mothers' new groups. In one case a subordinate male (a subadult) fathered a female's foal; all the others were sired by the dominant adult stallion of their mothers' breeding groups.

The inbreeding coefficients (f) of the females' progeny that were conceived after dispersal ranged from 0.002 to 0.281 (Fig. 4; median = 0.035). Of the 73 offspring, 51 (70%) were born to individuals related to each other less than in the third degree ($f < 0.0625$), 11 (15%) resulted from matings intermediate between third and second-degree relatives ($0.0625 \leq f < 0.125$) and 11 (15%) from the most consanguineous matings (between second or first-degree relatives; $f \geq 0.125$). Of the highly inbred offspring, one was sired by his mother's own father and the other 10 by a paternal half-brother of the dam. Five of these, including the foal born to the father–daughter pair, were sired by stallions that did not live in the groups where their mothers matured sexually. The mothers ($N=2$) of the other six foals each bred with a paternal half-brother that was present in their natal groups during their first months of life (the first 3 and 11 months, respectively). These two females were born in 1976, in the only existing group in that year (the founder harem); they had therefore associated at some stage with all the

Table II. The winter weight gain of foals with different levels of inbreeding

Level of inbreeding	Winter weight gain (kg)			N
	Mean	SD	Range	
Highest ($f \geq 0.250$)	3	16	-16-22	5
High ($0.125 \leq f < 0.250$)	15.8	17.2	-13-48	21
Medium to low ($f < 0.125$)	12.3	19.2	-21-65	54

Effect of inbreeding level: one-way ANOVA: $F_{2,77} = 0.98$, $P = 0.38$.

males. The females that bred with familiar and more distant relatives were also born before 1977.

The females ($N = 12$) that conceived their first (or two first) offspring prior to dispersal also avoided breeding with familiar males. None of these offspring ($N = 15$) were sired by adult stallions of their mothers' natal groups (eight females had their father as a breeding stallion, while the other four females were unrelated to the stallions). These 12 females did not breed with maternal brothers (half or full) with which they had at some stage associated as part of their mothers' entourage. Those that did breed with familiar paternal half-brothers (one case) or familiar more distant relatives were all born during the early part of the study (1974-1976), when there were no groups without familiar individuals. Of the 13 offspring whose fathers could be determined, 8 (61%) resulted from matings between distantly related individuals (Fig. 4; $0 \leq f < 0.0625$).

There was no significant negative effect of the level of inbreeding on the winter weight gains of the foals (Table II). However, the mean value for the few ($N = 5$) foals with $f \geq 0.25$, i.e. whose parents were at least full siblings or father and daughter, was much lower than for less inbred foals.

We conclude that after natal dispersal, females generally bred with only one male of their new groups. Few of the resulting offspring (15%) were highly inbred ($f \geq 0.125$). Even when the females conceived before dispersal, only 31% of their offspring were highly inbred. This reduction in inbreeding did not result from a tendency of the females to avoid breeding with close kin per se, but arose from their avoidance of breeding with

males of the groups into which they matured sexually. These (familiar) males were, of course, normally the father and full and half-brothers.

Costs of Dispersal

Mortality in this herd was minimal, so we could not measure the survival costs of dispersal for the females. We could, however, evaluate two potential reproductive costs: their age at first breeding and the survival of their progeny.

The age of females at first breeding

The fact that some females first reproduced before dispersing allowed us to test whether dispersal delayed the age at first breeding, and therefore caused a fitness cost. This was not the case since females that dispersed when nulliparous gave birth at ages similar to those that were still in their natal groups (median age = 34.5 versus 35 months; Mann-Whitney U -test: $z = 0$, $N_1 = 13$, $N_2 = 22$, NS).

Survival of progeny before and after dispersal

Since some females gave birth for the first time prior to dispersal, we tested whether natal transfer affected offspring survival. Virtually all foal mortality occurred within the first few days of life (Duncan 1992), so we calculated offspring survival to 1 week.

The survival rate of foals in their first week tended to be lower when their mothers were still in their natal groups (43%, $N = 7$) than when they had emigrated but not significantly so (81%, $N = 26$; G -test of independence: $G_{adj} = 3.32$, $df = 1$, $P = 0.068$). Of the females that had emigrated, four gave birth in their original groups but transferred on the same day to their new groups; their offspring all survived to 1 week.

The reasons why offspring survival may have been lower when females had not emigrated from their natal groups are unclear. The immediate causes of mortality could not be determined for six of nine foals, including the five born to females that had emigrated. The remaining three foals were abandoned by their mothers in the first few hours of life. The females that had not emigrated were not younger (median age = 36 versus 34.5 months; Mann-Whitney U -test: $z = 0.59$, $N_1 = 7$, $N_2 = 26$, NS), nor did they weigh less (median body

weight=320 versus 296 kg; $U=12$, $N_1=4$, $N_2=12$, NS), or were in worse condition (median condition score=2.5 versus 3; $U=36$, $N_1=4$, $N_2=20$, NS). It was not possible to test for inbreeding depression since blood samples were available for only two of the foals that died.

DISCUSSION

Functional Hypotheses and the Choice of the New Group

The tendency for young mares to transfer to particular groups did not appear to be influenced by the likelihood of reducing the level of competition they faced: none of the predictions based on the intra-sexual competition hypothesis was supported. Although they were more likely to disperse to groups smaller than their maternal groups, they did not selectively join groups with fewer resident females. Since the females were subordinate to all the resident mares in their natal groups (Monard et al., in press), and normally ranked lowest in the hierarchy of resident females in their new groups, dispersal did not, as a rule, lead to their attaining higher ranks. Furthermore, there was no tendency for females to disperse to groups with the fewest resident females, and they suffered more aggression from resident mares in their new groups than in their natal groups.

The competitive consequences of natal transfer have not been measured for females in other populations of harem-forming equids. However, newly immigrant young mares have also been reported to face relatively high levels of aggression from resident females in their new groups (feral horses: Berger 1986; plains zebras: Klingel 1967; mountain zebras: Joubert 1972; Penzhorn 1984) and to occupy low ranks (Klingel 1967; Penzhorn 1984). Among other polygynous group-living mammals, the role of intra-sexual competition in female dispersal appears to differ between species: female chimpanzees, *Pan troglodytes*, like these mares, receive more aggression from the females in their new groups than in their natal groups (Pusey 1980). In contrast, dispersing female mountain gorillas, *Gorilla gorilla beringei*, are more likely to transfer to groups with fewer resident females, joining lone males or groups with one female only (Harcourt 1978); and in this type of group there is no evidence that

they receive aggression from resident females (Harcourt 1979). Similarly, in red howler monkeys, *Alouatta seniculus*, young females may leave their natal groups when they contain two or more breeding females (Crockett & Pope 1993) and usually form new groups with one male and one female only (Pope 1989).

Though competition did not appear to influence the choice of the new group in this herd, several other factors did. The typical female transferred to a harem with one stallion and at least two subadult females. The immigration pattern of the young mares was also influenced by the distribution of previous transfers by familiar individuals of their maternal groups, which were normally close relatives (i.e. half or full siblings). When there was a choice, they preferred groups with familiar females; and, as predicted by the inbreeding avoidance hypothesis, they joined groups with no familiar males. Female Cape mountain zebras have also been observed to join harems containing familiar females (Penzhorn 1984).

Social and Genetic Consequences of Dispersal

Transferring to groups with familiar females or unfamiliar subadult females may have facilitated the integration of young mares into their new groups. The immigrant females were the target of high levels of aggression from the resident females of their new groups. Although they received low levels of aggression from the adult stallion (Monard 1992), they did not tend (at least initially) to associate preferentially with him, even though they were in oestrus at the time of transfer (Monard et al., in press). Instead, they formed close affiliative bonds, at least initially, with one familiar female or one unfamiliar subadult female of similar age and adjacent rank. Though these results are based on a small number of individuals (six), they contrast with those obtained on female chimpanzees, which tend to associate with males of their new group during the first few months following their entry, even when not in oestrus (Pusey 1980); and these males protect them from the aggression of resident females, which was not observed in this study. Immigrating females have been observed to remain close to the male(s), and receive protection from them in gorillas (Watts 1991, 1992), plains zebras (Klingel 1967) and mountain zebras (Penzhorn 1984), too. In the Camargue herd the dominant stallions of harems

maintained close, and apparently long-lasting, bonds with only one or two of the first females they acquired (C. Feh, unpublished data). This may explain why the six young females studied here, which all joined groups with two or more mares, did not form close bonds with the stallion.

The formation of close bonds with another female of the breeding group appeared more important for the young mares' integration than being herded by the stallion. The frequency of herding behaviour did not always peak at the time of immigration; young females were not in fact herded more often than adult mares with 5 years' residence in their breeding group (C. Feh, unpublished data; median frequency=0.41 times per h for older mares versus 0.33 for the young females; Mann-Whitney U -test: $U=13.5$, $N_1=4$, $N_2=7$, ns). Being herded by the stallion may, however, play a role, especially when the female transfer leads to the formation of a new harem; Kummer et al. (1981) noted a similar pattern in hamadryas baboons, *Papio hamadryas*.

The choice of groups with familiar females appeared to provide competitive advantages. When these were daughters of mares lower in rank than their own mothers, immigrating females tended to outrank them (thus inheriting maternal rank) and therefore did not occupy the bottom rank in the hierarchy of resident females, as was the case in other circumstances. Dominance relations within their natal groups between these pairs of females are unknown because no clear dominance relations could be detected between young females and the offspring of other mares (Monard et al., in press). It must be stressed that mares have never been observed aiding their daughters in contests against other members of their natal groups, which contrasts with some female-resident polygynous primates, where inheritance of maternal rank by daughters arises largely through kin females' support in contests (savanna baboons, *Papio cynocephalus*, macaques, *Macaca* spp., and vervets, *Cercopithecus aethiops*: reviewed in Walters & Seyfarth 1987; gelada baboons, *Theropithecus gelada*: Dunbar 1980). The mechanisms by which inheritance of maternal rank is acquired by young mares within their breeding groups are so far unknown. There was no indication that immigrant young mares formed alliances (i.e. aiding each other in contests against other mares, or forming coalitions sensu Cheney

1977) with familiar females or with higher-ranking females. In contrast, when closely related female mountain gorillas (mother-daughter or sisters pairs) live in the same group when adult, they do sometimes cooperate in competitive interactions against less-related adult females (Stewart & Harcourt 1987). Nevertheless, unlike female-resident species, young female gorillas do not acquire ranks adjacent to those of their mothers (see Harcourt & Stewart 1987, 1989 for further information).

The young mares in our study resemble immature male vervets, long-tailed macaques, *Macaca fascicularis*, and rhesus macaques, *M. mulatta*, which also disperse preferentially to groups with familiar same-sex individuals from their natal groups (reviewed in Pusey & Packer 1987a). The functional explanation for this preference in male cercopithecines is to some extent similar, since the presence of brothers or natal peers appears to facilitate young males' integration into their new groups.

The genetic consequence of transferring non-randomly to groups with familiar females but no familiar males was to increase the likelihood of joining groups with closely related mares and avoiding close-kin males: 59% of the young mares were related in the second or first degree to at least one resident mare of their new groups, whereas only 30% were as closely related to the breeding male(s). It is striking that the only females that transferred to groups with familiar males (paternal half-brothers or more distant relatives) were all born in the single group of the early years. In other populations of harem-forming equids and most other polygynous mammals, genetic relatedness between immigrant females and members of their new groups is unknown, but in gorillas female kin have been reported to transfer together to the same group (Stewart & Harcourt 1987). Thus even in female-emigrant species, female kin may remain together when possible.

Paternity analyses as well as observations of matings showed that once they had dispersed, young mares generally bred with only one male of their new group, normally the dominant stallion. As a result, their offspring were generally only slightly inbred. These findings provide further support for the inbreeding avoidance hypothesis.

The fact that some foals conceived after natal dispersal were highly inbred shows that females

avoided breeding with males of their most immediate social entourage when juvenile, not with close male relatives per se. The few females that conceived their first foals before dispersing also avoided breeding with familiar males. In particular, although they (and indeed other young females) were approached sexually while in oestrus by adult stallions of their natal groups (Monard et al., in press), none bred with such males regardless of whether these were related. Furthermore, the age at dispersal of females that had their fathers in their natal groups (median=23 months, range 12–42, $N=26$) did not differ significantly from the age of those whose fathers were not present (median=25 months, range 13–42, $N=13$; Mann–Whitney U -test: $z=1.03$, ns). These findings therefore provide no evidence for an inbreeding avoidance mechanism based on kin recognition by phenotype matching, such as has been found experimentally in some species of insects, amphibians, birds or rodents (for reviews see e.g. Fletcher & Michener 1987; Hepper 1991); rather it appears that avoidance of extreme inbreeding by females was based on prior association, which is the most commonly demonstrated mechanism underlying kin recognition in vertebrates (e.g. Blaustein et al. 1987). Natal dispersal in female horses therefore appears to be imposed by the reproductive strategies of males, in particular by long-term tenure of harems.

Non-random dispersal to groups with no familiar males may well have had genetic benefits. Though our data do not provide statistically significant evidence for inbreeding depression, there is a strong suggestion that this can occur in the most extreme cases of inbreeding (when $f \geq 0.25$). The only study of inbreeding depression in natural populations of mammals where paternity was determined using biochemical or molecular genetic methods (Hoogland 1992) did not demonstrate a negative effect either. Indeed inbreeding depression has so far been demonstrated in mammals only in captive or experimental populations, where the most highly inbred individuals (with $f \geq 0.25$) formed a considerable proportion of the samples (e.g. Ralls et al. 1979; Haigh 1983; De Bois et al. 1990; Laikre & Ryman 1991; Jiménez et al. 1994).

To conclude, there appeared to be both social and probably genetic benefits associated with a dispersal pattern in which young females transferred non-randomly.

Reproductive Consequences of Dispersal

Young mares in this herd suffered no reproductive costs from leaving their natal groups. First, even though there is evidence from various mammal species where females are typically philopatric, that females breeding in their natal area or group have higher reproductive success than those that disperse (e.g. Waser & Jones 1983; Pusey & Packer 1987b; Wiggett & Boag 1993), the young mares appeared to benefit from dispersing. Foals born to females that were still in their natal groups tended to have lower survival rates than those born to females that had emigrated, though this requires further field data as the result was not quite significant. Keiper & Houpt (1984) also observed in feral ponies that females still in their natal groups produced fewer living foals, and Rutberg & Keiper (1993) suggested that this could be due to inbreeding depression. Neither in their study nor in ours are the critical data (i.e. the inbreeding coefficients of the foals that died) available to test this hypothesis.

We found no obvious physiological explanation for this effect, since females that gave birth before transfer were of similar age, weight and body condition to those that had emigrated. There may be a social explanation: females still in their natal groups may have failed to develop a close attachment to their new-born foals because of their attachment to their own mothers. The two females for which quantitative data were available and which abandoned their foals had their mothers as their only preferred partner for proximities and for affiliative interactions given during the 2-month period just before they gave birth (Monard 1992); during the first few hours after parturition, they did not stay close to their foal as mares normally do (e.g. Tyler 1972), rather they followed their mother, leaving their new-born foal alone (A. M. Monard, personal observations).

Second, dispersal did not cause a delay in first reproduction in these female horses: females that dispersed when nulliparous produced their first foal at ages similar to those that first reproduced in their natal groups. There is a similar trend in gorillas (Watts 1991), which contrasts with group-living mammals where a significant proportion of females remain philopatric, such as lions (Pusey & Packer 1987b) and red howlers (Crockett & Pope 1993). In these species

females that leave their natal groups do suffer delays in breeding, which indicates a fitness cost of dispersal.

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