

INFLUENCE OF FAMILIARITY ON FREQUENCY OF INBREEDING IN WILD HORSES

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Received February 28, 1986. Accepted September 5, 1986

Data on mechanisms of inbreeding avoidance or on the frequency of incestuous mating in mammalian populations are uncommon (Cockburn et al., 1985; Hoogland, 1982; Packer, 1979; Pusey, 1980), and, for ungulates, they are lacking. Almost 100 years ago Edward Westermarck implicated familiarity as a possible mechanism; children who were reared together avoided mating with one another as adults (Westermarck, 1891). Recent experimental evidence for both humans, primarily from Israeli Kibbutzim (Shepher, 1983), and nonhumans (Bateson, 1983; Blaustein and O'Hara, 1982; Holmes and Sherman, 1983) suggests that associations at early ages influence later social behavior including breeding. Despite a strong body of theoretical expectations (Alexander, 1979; Bekoff, 1981; Moore and Ali, 1984), little empirical support for this idea exists from observations of wild mammals. Virtually nothing is known of the frequency that individuals who are reared together encounter or breed with one another as adults (but, see Hoogland, 1982). This problem generally arises because of the difficulty of acquiring information on the reproductive relationships among members of family groups once juveniles attain breeding ages, and because, in natural populations, it is rarely known which individuals are true fathers. Here we present data, made available by natural field experiments, that bear on this issue. We show that, for wild horses (*Equus caballus*) of the Great Basin Desert of North America, incestuous (father-daughter) matings sometimes occur, and that they result because individuals fail to remember others with whom they previously associated.

Methods, Social Organization, and the Experiment

Between 1979 and mid-1984 over 8,200 hours were spent observing wild horses in the Granite Range of Nevada, an insular fault-blocked mountain of about 500 km². The Granite Range is only one of several hundred mountain chains found in the Great Basin Desert of North America—an area with 40,000–60,000 feral horses (Berger, 1986). All animals at our study site were individually identifiable by distinct color characteristics. Ages of 146 of the 149 Granite horses were determined by one of the three following methods: 1) birthdates were known for animals five years of age or less; 2) ages of small horses (either foals or suspected yearlings) were estimated by size when the study began; 3) relative tooth-wear patterns were determined for 28 animals immobilized over a 16-month period (Berger et al., 1983).

Genealogies among females and their offspring were determined by direct observation of births or subse-

quent mother-young affiliations. Paternal relationships were established by observations of 244 copulations from which 92 foals were born. Stallions were identified as the true fathers when the median date of copulation during a mare's estrous cycle fell within a standard gestation length of Granite Range foals (345.1 ± 8.5 days for females, 348.3 ± 9.3 days for males; see Berger, 1986 for further details. Values presented here and throughout are $\bar{x} \pm SD$). In cases when two or more males copulated with the same female during the same estrous (2% of the total copulations), each was assigned equivalent paternal representations because of the uncertainty. However, for the data reported here, no offspring resulted from copulations by multiple males.

In wild horse societies, individuals occur in distinct year-round bands, each with at least one stallion who protects his harem (females and young) from bachelor males (Keiper, 1976). Copulations with harem females occur within the band (Rubenstein, 1981; Waring, 1983); that is, females do not move outside their bands to copulate with wandering males. Both sexes emigrate from their natal bands at about the time of puberty. At our study site, dispersal occurred at 2.16 ± 0.84 years of age in 32 females (range: 13–50 months) and 2.31 ± 0.88 years in 31 males (range: 11–52 months) (*t*-test, ns, *d.f.* = 61). Bachelor males are occasionally successful in taking over harems, and, as a result, stallions can be either the true fathers or the stepfathers of the young that grow up within their bands. Hence, through natural events, experimental situations are created where stallions associate for different lengths of time with young, some of whom they sired while others they have not. These fortuitous events allow examination of the hypothesis that length of prior association influences male mating responses to young females once they are (re-)encountered when sexually mature. We reasoned that if association was an important factor in recognition, stallions should copulate with pubescent females with whom they were not familiar and avoid those that were raised in their bands.

RESULTS

Do true fathers and stepfathers differ in their reproductive behavior toward young females who grow up in their bands? Of 32 young females that reached puberty, 24 were observed to copulate. Five of these females changed bands prior to puberty when they either accompanied their mothers to new bands or their natal bands were taken over by new stallions. The result was that five immature females attained puberty in bands with stallions who were not their true fathers. In none of the above 24 cases did true or stepfathers mate, or

even attempt to mate, with females that matured sexually within their bands despite ample opportunities to copulate with their pubescent true daughters or stepdaughters prior to their emigration (Table 1). In one instance, a pubescent female mated with an unfamiliar male while her father stood only 8 m away and ignored the copulation. On two other occasions, stallions stood less than 50 m away as their daughters mated with unfamiliar males.

The fact that stallions failed to discriminate when they refrained from mating with related and unrelated familiar young females offers tentative support for the idea that copulating with young from their harem is avoided through familiarity. Nevertheless, to demonstrate that familiarity per se is the important proximate factor promoting mating avoidance, it is necessary to show that non-harem males copulate more frequently with young (emigrating) females than do resident stallions. For, although the 24 young females were observed to copulate with 24 unfamiliar males, if unfamiliar males bred these females at sufficiently low rates when they encountered them, it would suggest that most males, regardless of familiarity, avoid mating with young females.

This idea was examined by comparing the frequency that nonresident males mated young familiar females (Table 1). We judged an encounter as any situation when unfamiliar males sniffed the ano-genital regions of young females that had emigrated from their natal bands. Of the 24 females observed copulating, four mated more than once with different males, while 12 mated with males upon first encounters (the remainder copulated upon secondary or subsequent encounters with strange males). Overall, 28 copulations occurred during 53 encounters with unfamiliar males (Table 1). Significantly more pubescent females were bred by unfamiliar males than by familiar ones ($G = 13.13$, $P < 0.001$, $d.f. = 1$). Therefore, our field observations provide evidence that familiarity is at least one, if not the most important, mechanism responsible for mating avoidance with young, a fact demonstrated by experimental studies of vertebrates (Holmes and Sherman, 1983; Bateson, 1983).

Later in life, true (or even step-) fathers failed to differentiate between sexually mature females with whom they were familiar as youngsters. For instance, two times true daughters were re-encountered as adults by their fathers who acquired them from different bands, situations which occurred at least 19 months after the females had emigrated from their natal bands (and fathers). In both cases these daughters were mated by their fathers and one inbred foal was born. There were no indications of recognition between these fathers and daughters as the stallions courted their daughters in the same manner as they did unrelated mares, and neither sex refrained from subsequent copulations. Thus, of the 129 matings in which genealogies were known, 3.9% of the copulations were between fathers and their genetic daughters.

Support for the idea, that early associations influence the behavior of stallions toward young later in life, can also be inferred from observations of stallion responses toward sons and non-sons. Like daughters, sons also emigrate from their natal bands (Rubenstein, 1981), usually between the ages of two and four years, and remain as bachelors (Keiper, 1976; Miller, 1981). These

TABLE 1. Summary of observed copulations by familiar (those of the same harem) and unfamiliar (either bachelors or stallions from other harems) males upon encountering females at their first estrus, compared with the number possible (from the number of encounters).

	Number of observed copulations by	
	Harem males	Non-harem males
Observed	0	28
Possible	24	53

males often try to acquire their own harems; as a result they (re-)encounter stallions. Because stallions can be either true fathers or stepfathers, opportunities exist to determine how prior association influences stallion behavior toward bachelors. Elsewhere (Berger, 1986) it was shown that stallion behavior was modified on the basis of prior association: 1) stallions responded aggressively to unfamiliar bachelors (rivals ?); but 2) stallions played with familiar bachelors (i.e., non-rivals ?). However, as with daughters, distinctions between familiar and unfamiliar males ceased after about 18 months (Berger, 1986). These observations indicate that stallions modified their later social interactions toward young that they once knew, and that such responses were independent of sex and genealogy.

DISCUSSION

When compared with prior studies, including those on horses, which either imply that young may leave genetically related conspecifics to avoid inbreeding (Feist and McCullough, 1976) or confirm that inbreeding coefficients are lower than expected based on random mating with respect to genealogy (Duncan et al., 1984), our results differ in three respects. First, they demonstrate that young females emigrated from bands in which they grew up, regardless of whether or not resident stallions were true fathers. Second, they show that the inbred mating occurred later in life and not when daughters reached puberty. Third, they show that natural situations occur in which individuals are born or grow up in groups where they are treated as kin although they have only associated with the members of the group and are not related genetically to them.

Although our data support the hypotheses that recognition is more likely to occur between stallions and young females which have previously associated, and that avoidance ensues more often when individuals are familiar with one another, it is not entirely clear which sex more actively promotes inbreeding avoidance. If it was the young females, they should offer stallions few opportunities for mating. The data support this idea since 100% of the young departed from natal bands when in estrus (although for unknown reasons 21% returned to natal bands after copulating). However, if stallions were responsible for inbreeding avoidance, they should refrain from copulating and not hinder breeding attempts by rival males with young familiar females. Our observations indicate that males avoided copulating even when they observed familiar young females mating. Thus, both sexes participated in the avoidance process.

Opportunities for similar behavior might also be expected in other mammalian groups with year-round harem social systems. For example, some males hold tenure for several years in carnivores (Bertram, 1975; Packer and Pusey, 1982) and primates (Hrdy, 1977; Dunbar, 1985), and possibly in a few rodents (Armitage, 1984) and bats (McCracken and Bradbury, 1981). Recognition between fathers, stepfathers, and their reproductive-aged daughters may also occur in these taxa due to associations in early life, but additional work will be necessary to determine the extent of such putative relationships and how they apply to the frequency of inbreeding.

ACKNOWLEDGMENTS

We thank the Harry Frank Guggenheim Foundation, the Bureau of Land Management, Smithsonian Institution's Conservation and Research Center, and the National Geographic Society for assistance. M. Rowe, S. Jenkins, J. Wehausen, G. Schaller, R. and N. Thornhill, and two anonymous reviewers offered valuable advice. M. Berbach, D. Dole, D. Daneke, A. Harris, P. Jancar, L. Roberts, R. Rudman, and C. Stockwell were splendid field workers.

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