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Reproductive effort and offspring sex ratio in female Przewalski horses *Equus przewalskii* (Mammalia: Equidae)

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Abstract: The frequency of foaling and its effect on the sex of newborn offspring were studied in female Przewalski horses. The results can be summarized as follows:
(1) Foaling frequency was higher than random in 4-7 year old mares. Subsequently it decreased to randomness, which remained stable until a very high age of the mares.
(2) Sex of the delivered foal had no effect on the reproductive performance of the mare in the following year.
(3) Reproduction or barrenness in the preceding year had no effect on the sex of the subsequent foal.
(4) These results do not agree with the Trivers-Willard hypothesis, while they appear to fit the Maynard Smith's (1980) assumption that the secondary sex ratio is fixed in many animal species.

The theory of sex allocation (Trivers & Willard 1973, Charnov 1982) predicts that parents in relatively good condition should invest more in individual offspring of the sex with greater variance in reproductive success, while the reverse is true for parents in relatively bad condition. Fisher (1930) assumed that this should be manifested in the secondary sex ratio (see also Trivers & Willard 1973, Burley 1982). Maynard-Smith (1980) developed an alternative model, according to which the secondary sex ratio is fixed, but parents may differently invest in their offspring after birth.

Captive Przewalski horses, *Equus przewalskii* Poljakov 1881, are a suitable object for testing these assumptions, because their reproductive patterns and simplified life conditions *a priori* exclude several factors which can obscure the relationship. In particular, they are strictly monotocous (Mohr & Volf 1984), so that variations in litter size are ruled out (*cf.* Myers 1978, Lloyd 1987); they are free of nutritional stresses (*cf.* Rivers & Crawford 1974, McGinley 1984); they do not suffer from predation (cf. Berger 1983a); and they have prolonged pregnancy, which prevents them from breeding more often than once per year (Veselovský & Volf 1965).

Trivers & Willard (1973) and others (Clutton-Brock & Albon 1982, Rutberg 1986) suggested that maternal condition is likely to be influenced by previous reproductive effort. For large mammals, such as horses, it means that females which skipped one year (or more years) of reproduction are likely to be in better-than-average condition (Trivers & Willard 1973, Rutberg 1986). A previous study failed to find the relation between the secondary sex ratio in Przewalski horses and any of the 8 considered variables, viz. maternal age, paternal age, parity, birth

sequence, female's predisposition, number of foals born to 3-6 year old mares, season and decade (Mlíkovský 1988); this paper, however, will focus on the relationships between barren years and the secondary sex ratio in the Przewalski horse.

Material and methods

All demographic data used in this paper were extracted from the published Pedigree Books of the Przewalski Horse (Volf 1980, 1981-1988). Thus, they consider captive animals. Overall, data on 282 females with 2-16 young were obtained. Standard statistical techniques were used in testing the results (Sokal & Rohlf 1969, Sachs 1974).

RESULTS

Relation between maternal age and foaling frequency

When a mare foaled, its reproductive status in the next year was recorded. Only those females which continued to reproduce after that particular year were taken into consideration. The results (Tab. 1) show that

TABLE 1. *Effect of reproducing at a given age on the reproductive performance in the subsequent year in Przewalski horse mares (see text for explanation).* Significance: - = $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Age (yr)	n	repeated reproduction n (%)	barrenness n (%)	χ^2	Sign.
2	1	0 (-)	1 (100)	-	-
3	80	44 (55.0)	36 (45.0)	0.612	-
4	121	74 (61.2)	47 (38.8)	5.587	**
5	153	10 (66.0)	52 (34.0)	15.059	***
6	146	92 (63.0)	54 (37.0)	9.377	**
7	129	79 (61.2)	50 (38.8)	6.078	**
8	116	69 (59.5)	47 (40.5)	3.802	-
9	90	54 (60.0)	36 (40.0)	3.211	-
10	92	56 (60.9)	36 (39.1)	3.924	*
11	89	52 (58.4)	37 (41.6)	2.202	-
12	71	38 (53.5)	33 (46.5)	0.225	-
13	58	40 (69.0)	18 (31.0)	7.603	**
14	64	29 (45.3)	35 (54.7)	0.391	-
15	32	22 (68.7)	10 (31.3)	3.781	-
16	45	24 (53.3)	11 (46.7)	3.200	-
17-19	72	36 (50.0)	36 (50.0)	0.014	-
20-22	31	14 (45.2)	17 (54.8)	0.129	-
23-24	6	0 (-)	6 (100)	5.143	*
Σ	1398	824 (58.9)	575 (41.1)	43.963	***

Przewalski horse mares foal more frequently in consecutive years between the ages of 4-7 years, which approximately coincides with the peak fecundity of this species (Mlíkovský, unpub. data), than later, when delivery of a foal had no statistically significant influence on barrenness or pregnancy in the subsequent year. It is remarkable that this randomness lasted until a very high age of the mare (Tab. 1). The seemingly non-random deviations at the age of 10 and 13 years are more probably statistical artifacts than real biological phenomena (*cf.* Gill 1985).

There is an almost complete absence of data on the foaling frequency in horses and their allies. Penzhorn (1985) and Penzhorn & Lloyd (1987) have found that median foaling interval in free-ranging Cape mountain zebras, *Equus zebra zebra*, was 25 months, and remarked that this rate remains stable until a high age in the mare. Similarly, Seal & Plotka (1983) reported than in feral horses, *Equus caballus*, at least 50% of the eligible mares were pregnant in consecutive years. These data support those presented in this study. Concordance of these results indicates (1) that the observed pattern of foaling frequency may be universal in the genus *Equus*, and (2) that it was not influenced by the conditions of captivity under which Przewalski horses live.

The causes of this pattern are less clear. Ball *et al.* (1985) observed that fertility rates are similar in normal and barren mares, so that the resulting barrenness is probably caused by early embryonic loss which is common in *Equus* females (Ball *et al.* 1985, Ginter *et al.* 1985, Villahoz *et al.* 1985, Forde *et al.* 1987, Woods *et al.* 1987). The causes of fetal loss are diverse and may include, e.g., energy-deprivation (Potter *et al.* 1987), or emotional disturbances, incl. social induction (van Niekerk & Morgenthal 1982, Berger 1983b). Unfortunately, relative contributions and interrelationships between these factors have not yet been investigated.

Effect of bearing son or daughter on the mare's reproductive performance in the following year

The sex of the newborn foal had no statistically significant effect on whether the mare reproductively skipped the following year (or more years) or whether it delivered another foal during the next year (Tab. 2). Only 6-year old mares foaled significantly more

TABLE 2: *Effect of the offspring sex on the reproductive performance of mares in the subsequent year (see text for explanation). F+, M+ = breeding one year after foaling a female or male, F-, M- = barren year after foaling a female or male.*
*Significance: - = p > 0.05, * = p < 0.05.*

Age (yr)	n	F+	F-	M+	M-	χ^2	Sign.
2	1	-	-	-	1	-	-
3	80	20	20	24	16	0.808	-
4	121	42	22	32	25	1.142	-
5	153	54	27	47	25	0.033	-
6	146	58	23	34	31	5.762	*
7	129	38	29	41	21	1.202	-
8	116	35	32	34	15	3.453	-
9	90	34	20	20	16	0.494	-
10	92	22	16	34	20	0.241	-
11	89	30	20	22	17	0.116	-
12	71	18	20	20	13	1.244	-
13	58	21	8	19	10	0.322	-
14	64	15	20	14	15	0.188	-
15	32	8	5	14	5	0.530	-
16	45	14	16	10	5	1.607	-
17-19	72	16	19	20	17	0.500	-
20-22	31	6	9	8	8	0.313	-
23-24	6	-	5	-	1	-	-
Σ	1398	431	313	393	261	1.176	-

TABLE 3: *Effect of the reproductive performance or barrenness on the sex of offspring foaled in the subsequent year (see text for explanation). +F, +M = female or male offspring foaled after a delivery of a foal in the previous year, -F, -M female or male offspring foaled after a barren year.*
*Significance: - = p > 0.05, ** = p < 0.01.*

Age (yr)	n	+F	+M	-F	-M	χ^2	Sign.
4	44	20	24	-	-	-	-
5	95	42	32	11	10	0.087	-
6	133	54	47	23	9	2.457	-
7	115	58	34	13	10	0.217	-
8	119	38	41	25	15	1.980	-
9	104	35	34	16	19	0.207	-
10	95	34	20	14	27	8.178	**
11	88	22	34	18	14	2.237	-
12	79	30	22	17	10	0.182	-
13	64	18	20	16	10	0.885	-
14	70	21	19	17	13	0.116	-
15	43	15	14	9	5	0.521	-
16	44	8	14	13	9	2.347	-
17	32	14	10	2	6	2.067	-
18	29	8	8	10	3	2.240	-
19-21	47	11	15	9	12	0.002	-
22-24	17	3	5	5	4	0.537	-
Σ	1218	431	393	218	176	0.857	-

frequently one year after having delivered female offspring than male offspring ($p < 0.02$), but this appears to be a statistical artifact without any biological meaning (*cf.* Gill 1985). To confirm the results obtained using the c^2-test, I have performed the non-parametric sign test after Dixon & Mood (Sachs 1974) which has yielded the same result (10+, 6-; $p>0.05$). There was also no trend in this phenomenon in relation to age of mares (run test, Sachs 1974; 9 runs in 16 age classes; $p > 0.05$).

In the only other observation of this sort, Clutton-Brock *et al.* (1981) showed that hinds of red deer, *Cervus elaphus,* who have reared sons are more likely to fail to breed the following year than those that have reared daughters. In contrast to this it seems that Przewalski horse mares invest (*cf.* Knapton 1984, Zeveloff & Boyce 1986) equally in male and female offspring, or if such a difference does exist (e.g in milk amount received by foals - Duncan *et al.* 1984), that it does not influence the body condition of mares to such a degree as to be manifested in their reproductive performance in the subsequent year. Reasons for the difference between Przewalski horses and red deer are not apparent at present.

Effect of barren years on the sex of the following foal

Skipping one or more years before producing a foal could be of some importance, because this could influence body condition of the mare (Trivers & Willard 1973, Rutberg 1986). However, no such relationship was found in Przewalski horse mares (Tab. 3). Again, the statistically significant result for age class of 10 years ($p < 0.05$) was more probably a statistical artifact than a biologically meaningful observation (*cf.* Gill 1985). Results of the c^2-tests were corroborated by the non-parametric sign test after Dixon & Mood (Sachs 1974): 11+, 6-; $p > 0.05$. Using a run test (Sachs 1974), no trend in relation to age of mares was detected (8 runs in 16 age classes; $p > 0.05$).

There are no comparable observations on horses and their allies. Clutton-Brock *et al.* (1982) found no

effect of barren years on the sex ratio of female's offspring in the next year in red deer, while Rutberg (1986) reported on the preponderance of male offspring among non-lactating cows of the American bison, *Bison bison* , thus supporting the Trivers-Willard hypothesis. The latter finding differs from the pattern found here in the Przewalski horses and by Clutton-Brock *et al.* (1982) in the red deer, where presence or absence of barren year(s) before delivery seems to have no detectable effect on the sex of the subsequent foal.

An evolutionary interpretation of these controversial results will be possible only after more relevant observations will be available.

CONCLUSIONS

Trivers & Willard's (1973) prediction that a relation exists between barren years and the secondary sex ratio in seasonally reproducing, monotocous animals was not corroborated for the Przewalski horse. The data thus seems to fit better Maynard Smith's (1980) hypothesis that the secondary sex ratio is fixed and parents may differently invest in their offspring of different sexes only after birth (see also Mlíkovský 1988). It is noteworthy, however, that data on some species support the Maynard Smith's hypothesis, while those on other species that by Trivers & Willard (see Clutton-Brock 1986a,b for review). This allows us to hypothesize that in some species the secondary sex ratio is fixed, while in others it is not, and/or that species are able to follow different reproductive strategies in different situations.

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