

Secondary sex ratio in the Przewalski horse *Equus przewalskii* (Mammalia: Equidae)

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Abstract

Sex ratio distribution in sibships and the relation between the secondary sex ratio and maternal age, paternal age, parity, birth sequence, season and year were studied in the Przewalski horse *Equus przewalskii*. No variations of the secondary sex ratio in relation to the studied factors were detected; sex ratio distribution was found to be simply binomial, i.e. random. The overall secondary sex ratio was found to be not significantly different from unity both in Przewalski horses and in other perissodactyls.

These data neither support, nor directly contradict, the theory that females are capable of adjusting the sex ratio of their offspring.

Introduction

Variations in the secondary sex ratio represent an important component of the TRIVERS and WILLARD's (1973) hypothesis of the adaptive value of the female's ability to adjust facultatively the sex of its offspring (see also BURLEY 1982), which in turn forms a part of the parental investment theory (TRIVERS 1972; MAYNARD SMITH 1977, 1980; CLUTTON-BROCK and ALBON 1982), and are thus of considerable theoretical interest. Despite this, data relevant to the problem are still rather scarce, even in mammals (CLUTTON-BROCK and ALBON 1982; BOLŠAKOV and KUBANCEV 1984; CLUTTON-BROCK 1986a) and birds (CLUTTON-BROCK 1986b). In the present paper I will contribute to the problem under discussion by analyzing the secondary sex ratio in the Przewalski horse *Equus przewalskii* Poljakov, 1881.

Captive Przewalski horses seem to be suitable for this purpose for the following reasons: They are strictly monogamous (MOHR and VOLF 1984), so that variations in the litter size are ruled out (cf. SMITH and FRETWELL 1974; MYERS 1978; GOSLING 1986b); they are free of nutritional stresses which were found to be important in this respect (cf. RIVERS and CRAWFORD 1974; McCLURE 1981; VAN DER MERWE and SKINNER 1982; SILK 1983; VERME 1983, 1985; MCGINLEY 1984); and they do not suffer from predation (cf. BERGER 1983). It could be thus expected that the effect of the remaining factors on the secondary sex ratio will be more pronounced and easier to detect.

Material and methods

All of the demographic data used in the present paper were extracted from the published Pedigree Books of the Przewalski Horse (VOLF 1980, 1981, 1982, 1983, 1984). They are, hence, considering captive animals. Overall, data on 1115 newborn foals were obtained, produced by 262 mares and 113 stallions. In testing the results, standard statistical procedures were employed (SOKAL and ROHLF 1969; SACHS 1974).

Results

Overall secondary sex ratio

Of the 1115 newborn Przewalski foals of known sex registered in the Pedigree Books 529 (= 47.44 %) were males and 586 (= 52.56 %) females. The slight preponderance of females is statistically not significant (see Tab. 1).

To see whether this is a specific feature of Przewalski horses, or whether the 1:1 secondary sex ratio is typical for horses and other perissodactyls, I compiled the relevant data from the "Mammals bred in captivity and multiple generation births" section of the International Zoo Yearbook, vols. 1-23 (Tab. 1). The data show convincingly that in not one of the listed species the secondary sex ratio significantly deviates from unity, although rhinos possess some tendency to bear more males than females ($p = 0.065$).

Effect of maternal age

The ability to parental investment varies with the female's age (CASWELL 1982, 1984), so that it could be expected that the secondary sex ratio will vary with the female's age as well. Indeed, such a variation has been reported for European bisons *Bison bonasus* (ZABLOCKI 1957), red deer *Cervus elaphus* (LOWE 1969), white-tailed deer *Odocoileus virginianus* (VERME 1983, 1985), barbary macaques *Macaca sylvanus* (PAUL and THOMMEN 1984),

Table 1. Overall secondary sex ratio in wild (w), feral (f) and captive (c) Perissodactyla

Taxon		N	N♂ (% ♂)	N♀ (% ♀)	$\frac{N♂}{N♀}$	G _{adj}	References
<i>Equus przewalskii</i>	c	1115	529 (47.44)	586 (52.56)	0.903	1.358	this study
<i>Equus caballus</i>	f	476	248 (52.10)	228 (47.90)	1.088	0.341	WELSH 1975; FEIST and McCULLOUGH 1975, 1976; BER- GER 1977, 1983; KEIPER 1979; NELSON 1980
<i>Equus hemionus</i>	c	772	400 (51.82)	372 (48.19)	1.075	0.438	this study
<i>Equus africanus</i>	c	72	36 (50.00)	36 (50.00)	1.000	0.028	this study
<i>Equus asinus</i>	f	23	7 (30.43)	16 (69.57)	0.438	1.113	McCORT 1979
<i>Equus zebra</i>	w	46	19 (41.30)	27 (58.70)	0.704	0.395	PENZHORN 1975
<i>Equus zebra</i>	c	276	141 (51.09)	135 (48.91)	1.044	0.029	this study
<i>Equus quagga</i>	w	216	114 (52.78)	102 (47.22)	1.118	0.232	SMUTS 1976
<i>Equus quagga</i>	c	2793	1340 (47.98)	1453 (52.02)	0.992	2.207	this study
<i>Equus grevyi</i>	c	622	323 (51.93)	299 (48.07)	1.080	0.389	this study
Equidae		6411	3157 (49.24)	3254 (50.76)	0.970	0.704	
<i>Tapirus indicus</i>	c	120	61 (50.83)	59 (49.17)	1.034	0.001	this study
<i>Tapirus terrestris</i>	c	446	225 (50.45)	221 (49.55)	1.018	0.004	this study
<i>Tapirus bairdi</i>	c	19	12 (63.16)	7 (36.84)	1.714	0.241	this study
<i>Tapirus pinchaque</i>	c	6	3 (50.00)	3 (50.00)	1.000	-	this study
Tapiridae		591	301 (50.93)	290 (49.07)	1.038	0.069	
<i>Rhinoceros unicornis</i>	c	37	24 (64.86)	13 (35.14)	1.846	1.122	this study
<i>Ceratotherium simum</i>	c	148	87 (58.78)	61 (41.22)	1.426	1.963	this study
<i>Diceros bicornis</i>	c	116	63 (54.31)	53 (45.69)	1.189	0.276	this study
Rhinocerotidae		301	174 (57.81)	127 (42.19)	1.370	3.388	

N = number of newborn animals sexed. G_{adj} = WOLF'S (1957) log likelihood ratio test, adjusted after YATES, two-tailed. No deviations are significantly different from unity ($p > 0.05$).

captive coypus *Myocastor coypus* (GOSLING 1986a), captive foxes *Alopex lagopus* (ŽEGALOV 1950), various species of domestic mammals (see BOL'ŠAKOV and KUBANCEV 1984 for review) and in man (e.g., MLÍKOVSKÝ 1987). On the other hand, no such variation was revealed in Przewalski horses (this study, Tab. 2) and in rhesus monkeys *Macaca mulatta* (RAWLINS and KESSLER 1986).

Effect of paternal age

In equids, males do not care for foals (GROVES 1974), so that no variation in the secondary sex ratio with the paternal age is to be expected on the basis of the parental investment theory. However, other mechanisms, such as physiological, may cause this relationship. The results show that the secondary sex ratio does not vary with the paternal age in Przewalski horses (Tab. 3), which agree in this respect with red deer (CLUTTON-BROCK et al. 1981) and domestic mice *Mus musculus* (SUNTZEFF et al. 1962). However, such a variation was described in pine martens *Martes martes* (GRAKOV 1969), various species of domestic mammals (KAMALJAN 1962; BOL'ŠAKOV and KUBANCEV 1984) and in man (e.g., POLLARD 1969; MLÍKOVSKÝ 1987).

Effect of parity

The effect of parity on the secondary sex ratio has been little studied thus far and seems to have no direct theoretical interpretation. Przewalski horses showed no variation of the secondary sex ratio with parity (Tab. 4). The same result has been reported also for rhesus monkeys (RAWLINS and KESSLER 1986) and domestic pigs *Sus scrofa* (KENNEDY and MOXLEY 1978; GRAY and KATANBAF 1985).

Table 2. Relation between the secondary sex ratio and maternal age (at delivery) in *Equus przewalskii*, based on the offspring of 262 mares

Age (Year)	N	N♂ (% ♂)	N♀ (% ♀)	$\frac{N♂}{N♀}$	χ^2_{adj}
2	1	1	—	—	—
3	60	28 (46.67)	32 (53.33)	0.875	0.001
4	104	54 (51.92)	50 (48.08)	1.080	0.668
5	117	60 (51.28)	57 (48.72)	1.053	0.547
6	108	49 (45.37)	59 (54.63)	0.831	0.112
7	91	44 (48.35)	47 (51.65)	0.936	0.005
8	91	37 (41.66)	54 (59.34)	0.685	1.417
9	78	30 (38.46)	48 (61.54)	0.625	2.174
10	73	46 (63.01)	27 (36.99)	1.704	6.490
11	69	29 (42.03)	40 (57.97)	0.725	0.608
12	57	26 (45.61)	31 (54.39)	0.839	0.021
13	45	21 (46.67)	24 (53.33)	0.875	0.002
14	49	23 (46.94)	26 (53.06)	0.885	0.005
15	29	15 (51.72)	14 (48.28)	1.071	0.076
16	38	12 (31.58)	26 (68.42)	0.462	3.224
17	22	12 (54.55)	10 (45.45)	1.200	0.206
18	22	7 (31.82)	15 (68.18)	0.467	1.572
19–20	23	13 (56.52)	10 (43.48)	1.300	0.066
21–24	27	13 (48.15)	14 (51.85)	0.929	0.091

N = number of sexed newborns. χ^2 test, adjusted after YATES, two-tailed. No deviations from the mean sex ratio are statistically significant ($p > 0.05$), excepting in 10 year old females, which tended to bear more sons than daughters ($0.05 > p > 0.01$). However, the 9 year old females showed the opposite (though statistically insignificant) tendency and after combining the two years together, no more deviation was apparent ($76♂ : 75♀$; $\chi^2_{adj} = 0.397$; n.s.). Such seeming statistical deviations are expected to occur on statistical grounds (HILL 1985).

Table 3. Relation between the secondary sex ratio and paternal age (at foal's birth) in *Equus przewalskii*, based on the offspring of 113 stallions

Age (Year)	N	N♂ (% ♂)	N♀ (% ♀)	$\frac{N♂}{N♀}$	χ^2_{adj}
3	8	2 (25.00)	6 (75.00)	0.333	0.853
4	34	16 (47.06)	18 (52.94)	0.889	0.013
5	79	38 (48.10)	41 (51.90)	0.927	0.001
6	96	47 (48.96)	49 (51.04)	0.959	0.030
7	101	48 (47.52)	53 (52.48)	0.906	0.009
8	91	42 (46.15)	49 (53.85)	0.857	0.034
9	108	58 (53.70)	50 (46.30)	1.160	1.398
10	93	43 (46.24)	50 (53.76)	0.860	0.023
11	76	30 (39.47)	46 (60.53)	0.652	1.681
12	66	25 (37.88)	41 (62.12)	0.610	0.358
13	56	33 (58.93)	23 (41.07)	1.435	0.420
14	49	22 (44.90)	27 (55.10)	0.815	0.053
15	40	19 (47.50)	21 (52.50)	0.905	0.023
16	38	17 (44.74)	21 (55.26)	0.810	0.035
17	32	14 (43.75)	18 (56.25)	0.778	0.065
18	32	14 (43.75)	18 (56.25)	0.778	0.065
19	25	15 (60.00)	10 (40.00)	1.500	0.419
20	26	13 (50.00)	13 (50.00)	1.000	0.003
21	22	12 (54.55)	10 (45.45)	1.200	0.196
22	16	8 (50.00)	8 (50.00)	1.000	0.003
23-27	18	10 (55.56)	8 (44.44)	1.250	0.197

N = number of sexed newborns. χ^2 test, adjusted after YATES, two-tailed. No deviations from expected distributions are statistically significant ($p > 0.05$).

Table 4. Relation between the secondary sex ratio and parity in *Equus przewalskii*

Birth sequence	N	N♂ (% ♂)	N♀ (% ♀)	$\frac{N♂}{N♀}$	χ^2_{adj}
1	260	125 (48.08)	135 (51.92)	0.926	0.021
2	195	99 (50.77)	96 (49.23)	1.031	0.738
3	158	81 (51.27)	77 (48.73)	1.052	0.780
4	122	49 (40.16)	73 (59.84)	0.671	2.307
5	100	46 (46.00)	54 (54.00)	0.852	0.035
6	85	37 (45.12)	45 (54.88)	0.822	0.376
7	60	31 (51.67)	29 (48.33)	1.069	0.277
8	46	24 (52.17)	22 (47.83)	1.091	0.245
9	33	15 (45.45)	18 (54.55)	0.833	0.003
10	21	8 (38.10)	13 (61.90)	0.615	0.736
11-15	32	14 (43.75)	18 (56.25)	0.778	0.175

N = number of sexed newborns. χ^2 test, adjusted after YATES, two-tailed. No deviations from the mean sex ratio are statistically significant ($p > 0.05$).

Effect of birth sequence

Sex sequences in individual families were investigated in man only so far, where they were found to be random in several studies (RENKONEN 1956; EDWARDS 1961, 1962; LOYD and GRAY 1969) and non-random in other ones (SCHÜTZENBERGER 1949, 1950; GRAY and MORRISON 1974). No deviation from randomness was revealed in Przewalski horses, where sex sequences were studied in families of 122 females with 4-15 foals ($\epsilon = 0.184$, $p > 0.1$; non-parametric run test after WALD and WOLFOWITZ 1940; cf. KLAT 1983).

Effect of the female's predisposition

The female's predisposition to bear either more daughters or more sons can be detected by an analysis of the sex ratio distribution in litters or families (sibships). The expected statistical distribution of the sex ratio within litters or families is the binomial one (EDWARDS 1960, 1962; HARMSSEN and COOKE 1983). The randomness of the sex ratio distribution in litters or families was corroborated in Przewalski horses (this study,

Table 5. Sex ratio distribution in sibships of *Equus przewalskii*

Sibship size	No. of litters	♂:♀	No. of litters		χ^2			
			observed	expected				
2	195	2:0	41	43.89	0.673			
		1:1	103	97.25				
		0:2	51	53.87				
3	160	3:0	22	18.27	1.959			
		2:1	51	58.13				
		1:2	65	61.66				
		0:3	22	21.80				
4	122	4:0	5	6.34	3.358			
		3:1	32	27.76				
		2:2	39	45.56				
		1:3	39	33.24				
		0:4	7	9.10				
5	100	5:0	3	16	9.99	5.643		
		4:1	13					
		3:2	22					
		2:3	37					
		1:4	21					
		0:5	4					
6	80	6:0	1	7	7.01	4.062		
		5:1	6					
		4:2	16					
		3:3	18					
		2:4	27					
		1:5	10				12	10.77
		0:6	2					
7	59	7:0	0	11	10.42	0.521		
		6:1	2					
		5:2	9					
		4:3	16					
		3:4	16					
		2:5	10					
		1:6	4				6	5.13
		0:7	2					
8	45	8:0	0	4	5.43	3.429		
		7:1	1					
		6:2	3					
		5:3	9					
		4:4	15					
		3:5	9					
		2:6	7				9	7.73
		1:7	2					
		0:8	0					

χ^2 test, two-tailed. No deviations from expected distributions are statistically significant ($p > 0.05$).

Tab. 5), dairy cattle *Bos taurus* (GRAY and HURT 1979), Siberian tigers *Panthera tigris altaica* (MLÍKOVSKÝ 1985) and in several studies on man (EDWARDS and FRACCARO 1958, 1960; GRAY and MORRISON 1974; GRAY and BORTOLOZZI 1977). On the other hand, some controversial indications exist that the sex ratio distribution in litters or families deviates from the binomial one in man (GEISSLER 1889; EDWARDS 1958), coypus (GOSLING 1986a), domestic pigs (GRAY and KATANBAF 1985) and in several other species of domestic mammals (GINI 1951; JAMES 1975).

Effect of the female's body condition

Direct data on body condition of pregnant Przewalski mares were not available, but TRIVERS and WILLARD (1973) have assumed that in large mono- or oligotocous mammals, the female's body condition is higher when the female has skipped reproduction in the foregoing year. Using this measure, no effect of the female's body condition on the secondary sex ratio of that female's offspring was detected in Przewalski horses (Tab. 6) but, using another measure, SKOGLAND (1986) revealed this effect in reindeer *Rangifer tarandus*.

Table 6. Relation between the secondary sex ratio and reproductive effort (measured as number of foals born to 3-6 year old mares) in *Equus przewalskii*

No. of foals	N	N♂ (% ♂)	N♀ (% ♀)	$\frac{N♂}{N♀}$	χ^2_{adj}
1	60	33 (55.00)	27 (45.00)	1.222	0.409
2	119	55 (46.22)	64 (53.78)	0.859	0.004
3	126	60 (47.62)	66 (52.38)	0.909	0.016
4	16	7 (43.75)	9 (56.25)	0.778	0.032

Mares which died before 6 year old were excluded from the analysis. N = number of sexed newborns. χ^2 test, adjusted after YATES, two-tailed. No deviations from the mean sex ratio are statistically significant ($p > 0.05$).

Seasonal variations

There is a distinct, though extended, foaling season in captive Przewalski horses in the Palearctic (MOHR and VOLF 1984), where 1103 of the 1115 registered Przewalski foals were born. Hence, it could be hypothesized that the secondary sex ratio will show some seasonal variation. However, no such variation was detected (Tab. 7). BAUMGARTNER (1985), who studied the same relationship in domestic hens *Gallus gallus* f. *domestica*, has found such a variation in one of the two strains he studied, but not in the other one. On the other hand, a strong seasonal variation in the secondary sex ratio was found in grey seals *Halichoerus grypus* (COULSON and HICKLING 1961) and in captive coypus (GOSLING 1986a).

Annual variations

Year to year variations in the secondary sex ratio were reported for a number of mammalian species, including, for example, American buffalos *Bison bison* (MCHUGH 1959), European bisons (KOROČKINA 1968) and water buffalos *Bubalus bubalis* (FISCHER 1966; COSWAMI and NAIR 1968). However, no such variation was observed in Przewalski horses (this study, Tab. 8).

Table 7. Relation between the secondary sex ratio and season in *Equus przewalskii*

Month	N	N♂ (% ♂)	N♀ (% ♀)	$\frac{N♂}{N♀}$	χ^2_{adj}
I	17	9 (52.94)	8 (47.06)	1.125	0.028
II	15	8 (53.33)	7 (46.67)	1.143	0.025
III	35	20 (57.14)	15 (42.86)	1.333	0.843
IV	148	67 (45.27)	81 (54.73)	0.827	0.328
V	358	176 (49.16)	182 (50.84)	0.967	0.162
VI	260	119 (45.77)	141 (54.23)	0.844	0.416
VII	123	56 (45.53)	67 (54.47)	0.836	0.202
VIII	55	28 (50.91)	27 (49.09)	1.037	0.092
IX	41	20 (48.78)	21 (51.22)	0.952	0.003
X	27	15 (55.56)	12 (44.44)	1.250	0.357
XI	11	5 (45.45)	6 (54.55)	0.833	0.018
XII	13	6 (46.15)	7 (53.85)	0.857	0.022

N = number of sexed newborns. χ^2 test, adjusted after YATES, two-tailed. No deviations from the mean sex ratio are statistically significant ($p > 0.05$).

Table 8. Temporal changes of the secondary sex ratio in *Equus przewalskii*

Period	N	N♂ (% ♂)	N♀ (% ♀)	$\frac{N♂}{N♀}$	χ^2_{adj}
1901-10	13	5 (38.46)	8 (61.54)	0.625	0.165
1911-20	32	13 (40.63)	19 (59.37)	0.684	0.423
1921-30	36	15 (41.67)	21 (58.33)	0.714	0.343
1931-40	38	23 (60.53)	15 (39.47)	1.533	1.938
1941-50	25	10 (40.00)	15 (60.00)	0.667	0.352
1951-60	69	31 (44.93)	38 (55.07)	0.816	0.143
1961-65	90	45 (50.00)	45 (50.00)	1.000	0.083
1966-70	104	58 (55.77)	46 (44.23)	1.261	2.256
1971-75	162	71 (43.83)	91 (56.17)	0.780	0.934
1976-80	297	138 (46.46)	159 (53.54)	0.868	0.200
1981-83	246	124 (50.41)	122 (49.59)	1.016	0.509

N = number of sexed newborns. χ^2 test, adjusted after YATES, two-tailed. No deviations from the mean sex ratio are statistically significant ($p > 0.05$).

Discussion

Whether adaptive adjustment of the secondary sex ratio occurs in birds and mammals is still inconclusive (WILLIAMS 1979; CHARNOV 1982; CLUTTON-BROCK and ALBON 1982), because the relevant data are highly controversial. Since many factors may directly or indirectly affect the secondary sex ratio in higher vertebrates, it is favorable to study its variations experimentally (e.g., McCLURE 1981; MYERS et al. 1985; LABOV et al. 1986) and/or to select for the study such species or populations which are naturally independent of some of the possible factors (e.g., RUTBERG 1986). As shown above, captive Przewalski horses are suitable for such a kind of research. Despite that, none of the investigated factors, viz. maternal age, paternal age, parity, birth sequence, female's predisposition, female's body condition, season and year, proved effective.

To conclude, nothing was found in the variations of the secondary sex ratio in the Przewalski horse in support of the TRIVERS and WILLARD's (1973) sex adjustment hypothesis. However, it should be noted at the same time that two other important factors were not investigated in the present study, particularly the effect of the time of fertilization

within the estrus cycle (JAMES 1976, 1983; VERME and OZOGA 1981) and the effect of the social status of the female in the herd (SILK et al. 1981; SIMPSON and SIMPSON 1982; CLUTTON-BROCK 1982; CLUTTON-BROCK et al. 1984, 1986). Hence, the results reached, though not supporting the TRIVERS and WILLARD's (1973) hypothesis, cannot be used as a proof of its incorrectness.

Zusammenfassung

Das sekundäre Geschlechterverhältnis beim Przewalski-Pferd, Equus przewalskii (Mammalia: Equidae)

Das sekundäre Geschlechterverhältnis, seine Verteilung in Familien und die Beziehungen zwischen dem sekundären Geschlechterverhältnis und dem Alter von Mutter und Vater, der Parität, Geburtsfolge, Jahreszeit und Jahr wurden bei Przewalski-Pferden untersucht. Die Verteilung des Geschlechterverhältnisses wich von einer Binomialverteilung nicht signifikant ab. In dem sekundären Geschlechterverhältnis wurden keine Variationen entdeckt. Es wich weder bei Przewalski-Pferden noch bei anderen Perissodactylen signifikant von 1:1 ab.

Diese Angaben unterstützen weder die Theorie, daß die Weibchen das Geschlecht ihrer Nachkommen beeinflussen können, noch widersprechen sie ihr direkt.

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