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## Variations in the birth sex ratio and neonatal mortality in a natural herd of horses

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**Abstract** Variations in birth sex ratios and sex differences in juvenile mortality occur in a number of mammalian species, and in many cases have been linked to resource availability. Most of these biases in offspring sex ratios concern polygynous species with pronounced sexual dimorphism, and where females only are philopatric. Data on species with unusual life-history strategies, such as slight sexual dimorphism or dispersal by both sexes, are of particular interest. In this study of a natural herd of horses (*Equus caballus*) which experienced an eruptive cycle, and therefore a period of nutritional stress, male offspring had higher neonatal mortality rates in nutritionally poor years than in good ones, whereas “year quality” had no effect on the mortality of female offspring; year quality could therefore be used by mares as predictor of sex-specific offspring survival. We show that the environmental conditions that predicted lower survival of males were negatively related to their production: the birth sex ratio the following year was female-biased; and mares were less likely to produce a son when they had produced a son the preceding year. There was no significant effect of mother’s parity, age or rank, or the timing of conception or birth on offspring sex ratios. The mechanism leading to biases in the birth sex ratio could have been the loss of male embryos by mares that did not foal. As there was no evidence for selective abortion of male fetuses in females that did foal the next year, it is not necessary to invoke maternal adjustment, though this remains a

possibility. Finally, there was a suggestion that male offspring were more costly to raise than females, since mothers that reared a son in poor years tended to experience an increase in the interbirth interval between their two subsequent offspring.

**Key words** Birth sex ratio · Neonatal mortality · Resource availability · Horses

### Introduction

Adaptive biases in offspring sex ratios have been predicted by a number of theoretical studies (e.g. Trivers and Willard 1973; Clark 1978; Maynard Smith 1980; Silk 1983). Biased birth sex ratios and differential juvenile mortality have indeed been documented in a variety of animals: among these, mammals are of particular interest since there is now considerable observational and experimental evidence that variations in this class are related to resource availability (see Clutton-Brock et al. 1985; Clutton-Brock and Iason 1986; Clutton-Brock 1991).

The data available show that the directions of biases in birth sex ratios are often inconsistent, both within and across species. It therefore appears that many factors may affect birth sex ratios, directly or indirectly. It is likely that more than one mechanism is involved, and it has rarely been possible to distinguish between variations in offspring sex ratios which are due to maternal adjustment and those which are due to the consequences of sexual selection (see Clutton-Brock 1991 for a full treatment of these issues).

In addition to manipulating the birth sex ratio, parents could also vary the sex ratio of their offspring by manipulating juvenile survival. There is at the moment no evidence that this, energetically wasteful, mechanism is used (Clutton-Brock 1991). Nonetheless, variations in juvenile survival are commonly important components of variance in the reproductive success of mammals

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(Clutton-Brock 1988), and it has been argued that predictors of offspring survival should be among the strongest predictors of offspring sex ratio adjustment at birth (Wasser and Norton 1993).

Two main adaptive explanations for variations in offspring sex ratios have been proposed. The model of Trivers and Willard (1973) predicts that in circumstances where maternal investment influences the reproductive success of one sex more than the other, then mothers in good condition should produce offspring with birth sex ratios biased in favour of that sex. An alternative model, the local resource competition (Clark 1978; modified by Silk 1983), postulates that sex-biased dispersal could lead to long term costs in the production of offspring of the philopatric sex through competition for resources. Females in poor condition should therefore produce more offspring of the dispersing sex, while those in good condition could afford the postweaning costs of producing offspring of the philopatric sex.

Most of the studies of variations in birth sex ratios and juvenile survival concern polygynous species with pronounced sexual dimorphism, and where females only are philopatric: the inconsistency in the direction of sex ratio biases in these species (see above) could arise because both the Trivers and Willard process and local resource competition are involved, exerting selective pressures in opposite directions so that one process predominates within a particular species or population (see van Schaik and Hrdy 1991). Data on polygynous species showing slight sexual dimorphism, and on species in which both sexes disperse, so the local resource competition model can be eliminated, are therefore of particular interest (see Maynard Smith 1980).

A recent study of a slightly dimorphic species, the Asiatic wild ass (*Equus hemionus*), showed a biased birth sex ratio (Saltz and Rubenstein 1995). Females living in a stressful environment, the Negev Desert, were found to have an offspring sex ratio which was age-dependent, being significantly lower in animals which could be expected to be in poorer body condition, young and old mares, than in prime age ones.

We report here the results of a long term study on a closely monitored herd of another equid, the horse (*E. caballus*), which is also polygynous, slightly dimorphic and where both sexes disperse (e.g. Feh 1990; Monard et al. 1996). This herd went through an eruptive cycle, giving an opportunity to test for variations of the secondary sex ratio and juvenile mortality in a context of varying food availability.

Horses, like plains and mountain zebras (*E. burchelli* and *E. zebra*), are group-living ungulates whose mating system is based on one-male harems (Klingel 1974). They show slight sexual dimorphism in adult body weight (in this herd 5%); and male foals are heavier at birth (domestic horses: Hintz et al. 1979) and in this herd spent more time suckling between birth and six weeks of age and were more active (Duncan et al. 1984), so they may require more maternal care. Furthermore, reproductive success in the herd studied here varied more among males

(0–32 offspring from birth to 11 years, median = 10,  $n = 11$ ; Feh 1990) than females (7–11 offspring, median = 9,  $n = 10$ ; see also Berger 1986). High-ranking mares, which had higher-quality diets than lower-ranking ones (Duncan 1992, p. 91), produced sons with higher reproductive success (Feh 1990) and daughters that bred one year earlier in nutritionally poor years (Duncan 1992, p. 166). Maternal rank therefore influences offspring reproductive success, and is likely to have a greater effect on the success of sons, given the difference in variance. This species therefore appears to fulfil the requirements of the model of Trivers and Willard.

We examine birth sex ratios in relation to different environmental and maternal factors which could affect female condition, and test the following predictions: (1) that birth sex ratios vary in relation to mothers' age; (2) that birth sex ratios are low after nutritionally poor years; (3) that high-ranking mares produce an excess of male offspring; and (4) that producing a son should make it less likely that a mother will produce another in the next 2 years. We also test for an effect of the timing of conception (before or after the median date) on birth sex ratios; and for a differential cost in the production of male and female offspring.

The same variables were used in the analysis of juvenile mortality; we predict: (1) lower mortality in foals of prime age mothers; (2) higher mortality, particularly of male foals, in poor years; (3) higher mortality in foals, especially males, of low-ranking mares; and (4) higher mortality in foals born after raising a male.

## Methods

### Study animals and area

The data concern a herd of horses of the Camargue breed (a stallion, six mares and seven young horses) which was left unmanaged from December 1973 on the Tour du Valat estate in the south-east of the Camargue, France; it went through an eruptive cycle with numbers rising to nearly 100 in 1981. Minimal management was then applied: any very thin animals were removed and cared for elsewhere. The herd size was maintained at 50–60 until 1986 and at about 30 thereafter, and sex and age ratios were kept at levels typical of harem-forming equid populations with the adult sex ratio equal and 40% subadult animals (see Welsh 1975; Smuts 1976; Berger 1986). The herd was left undisturbed between round-ups for research or management purposes. In 1974 the social structure was similar to that of domestic herds (Wells and von Goldschmidt-Rothschild 1979) with only one large group and a solitary subadult male. In 1977 a more natural social system developed similar to that found in feral horses and plains and mountain zebras (Klingel 1974), with four harems and a bachelor group. This process continued rapidly, so that there were 12 groups, the maximum number, in 1981.

All horses were individually known, and monitored on most days, so the dates of births and deaths were usually known exactly, and the errors were never more than  $\pm 2$  days. By observing changes in the mares, the state of their abdomens and mammary glands, we knew when births were close, and blood on the hind-quarters and a flatter abdomen were taken as indicating that a birth had occurred. Females reached sexual maturity at 1–3 years, usually at 2 years, and produced one foal at a time. The mean gestation period in horses is 11 months (Ginther 1979).

Between 1973 and 1981 the horses were kept permanently in a semi-natural pasture of 335 ha (see Bassett 1978; Duncan 1992). As their numbers increased, the food resources declined and so did the body weight and condition of the horses. From autumn 1982 reserve pastures of 200 ha were used intermittently. The body condition of each horse was recorded monthly from October 1978 to April 1988, using a visual index (see Henneke et al. 1983) with six categories from 1 (excellent) to 6 (emaciated; Duncan 1992, p. 154). Data on body weights for all horses were available twice a year in autumn and spring, from September 1979 until September 1986. Foal birth weights were not measured. The median condition class of the breeding mares in March was 2–3 ("normal" to "moderate") except for 1981–1983 and 1985 (Fig. 1), in which the median condition class was 4 or 5 ("thin" or "very thin"). Trends in body weights were similar. The years were divided into two classes of "year quality" on the basis of condition: 1981–1983 and 1985 were classed as "poor" and the others as "good". There were no data on condition for the month of March in the early years (1974–1978), but the horses were at such low densities that the great majority were in moderate to good condition, so these years were classed as "good". The 1985 winter was the coldest in the last 30 years (Hellman index of winter severity, Ridgill and Fox 1990, calculated on data from the Tour du Valat meteorological station), which may have contributed to the poor state of the animals compared to the years before and after.

The individual condition scores and weights were not used in the analyses of offspring sex ratios for two reasons: first, the females' condition at the key moments in their reproductive histories was not known (e.g. conception, because the gestation length in mares varies by at least  $\pm 15$  days (Waring 1983); and birth, because the condition of the females was recorded only monthly); and secondly, data on condition and weight were available for only a sub-set of the years. Further, the condition data were not appropriate for the study of fine variations because of their imprecision, with only six classes: a direct measure of body reserves (e.g. ultrasonic) would have been more appropriate. The individual condition data were used across periods of gestation and lactation to test for differential costs of male and female offspring, using covariance analysis.

Births occurring in the first year were excluded from these analyses because the foals were conceived before the herd was established. A total of 222 foals were born during the 15 years (1975–1989) by 44 different females; of these foals the sex of 7 was not known. The median birth dates were between early March and late April. Social ranks of the mares were determined as described in Monard et al. (1996).

## Analyses

The timing of a conception or a birth was classed as early or late by comparison with the median for all mothers in that year. The mares

were divided into three age classes: we considered females less than 7 years as "young" as they had not completed their body growth (Duncan 1992, p. 156); as in Saltz and Rubenstein (1995) females were considered as prime until 12 years, and old thereafter. They were also divided into three classes of dominance rank: 1 = the highest-ranking mare, 2 = ranks 2 or 3, and 3 = ranks 4–9.

The statistical effects of the different variables on the birth sex ratio and the juvenile mortality of the two sexes were modelled using logistic regressions with the weighted-least-squares method of the CATMOD procedure (SAS Institute 1989). Complete models were built by introducing all variables with interactions and removing the non-significant terms step by step. Since we used data on foals born to the same mothers in different years, we tested for a "mare" effect on the birth sex ratio, restricting the analysis to females that produced nine or more foals to include reasonable numbers of foals per female (i.e. 10 females with 9–13 offspring); none was detectable (univariate logistic regression:  $\chi_2 = 10.88$ ,  $df = 9$ ,  $P = 0.28$ ).

To test for a differential cost of raising a male or a female offspring, we used covariance analysis in the GLM procedure (SAS Institute 1989) on the mares' condition scores across full lactation and gestation periods (covariates), with the sexes of the suckled and gestated offspring as factors (mares commonly conceived within a month of parturition; lactation lasted on average 9–10 months, Duncan et al. 1984). Complete models were built by introducing all variables with interactions and removing the non-significant terms step by step. The effects of seasonal and annual variations in condition were removed by expressing the data relative to the mean condition of all mothers for a given month within each year. Condition scores were log-transformed to normalise their distribution.

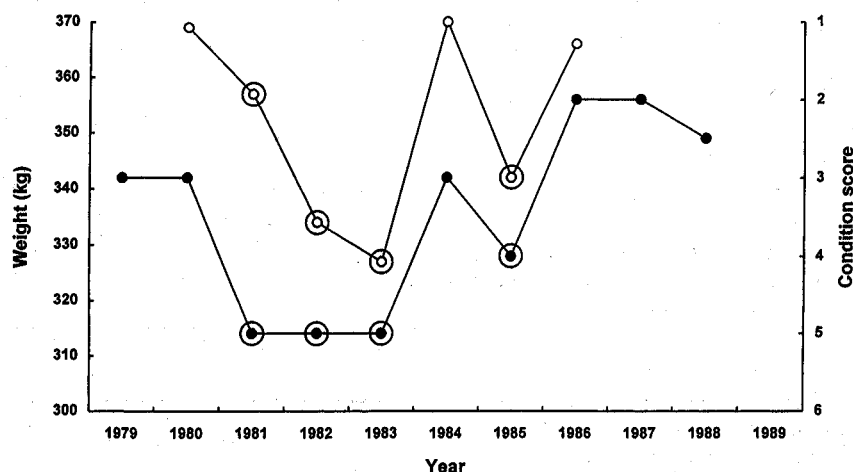
All tests were two-tailed and differences were considered significant at  $P < 0.05$ .

## Results

### Birth sex ratio

The overall birth sex ratio did not deviate significantly from unity (109 males and 106 females;  $G$ -test:  $G_{adj} = 0.042$ ,  $df = 1$ ,  $P = 0.84$ ), and varied across years, from 17 to 78% males (Table 1). Using the whole data set, mother's parity had no effect on the birth sex ratio (Table 2; univariate logistic regression:  $\chi_2 = 0.12$ ,  $df = 1$ ,  $P = 0.73$ ); mother's age had no significant effect either (Table 2; univariate logistic regression:  $\chi_2 = 0.49$ ,  $df = 2$ ,  $P = 0.78$ ), and there was no suggestion that

**Fig. 1** The median condition score (●) of multiparous mares in March of the years 1979–1988 (1 = excellent); median body weights of mares aged > 6 years (○) in March/April, less the estimated conceptus weight (see Duncan 1992, p. 253) are also given where these were measured. "Poor" years are circled



**Table 1** Foals born in the years 1975–1989, and the number of mares aged > 2 years that did not foal

Year of birth	Males	Females	% Males	Unknown sex	Mares with no foal
1975	1	5	17	0	0
1976	4	5	44	0	0
1977	6	3	67	0	1
1978	8	7	53	1	1
1979	10	10	50	1	1
1980	13	10	57	0	0
1981	15	10	60	2	0
1982 <sup>a</sup>	7	10	41	0	3
1983 <sup>a</sup>	4	8	33	0	4
1984 <sup>a</sup>	6	8	43	0	2
1985	7	11	39	1	0
1986 <sup>a</sup>	4	8	33	2	2
1987	9	6	60	0	0
1988	8	3	73	0	1
1989	7	2	78	0	3

<sup>a</sup> These conceptions occurred in a nutritionally poor year

prime age females produced more males than young and old ones.

Using the foals for which all data were available, we then tested for effects of the variables year quality at conception, timing of conception, mother's rank at conception, sex of the offspring of the previous year, and sex of the offspring reared 2 years before. Only year quality and the sex of the previous offspring were significantly related to birth sex ratio. Mares had a lower probability of producing a son after a poor year than after a good one; and after a poor year they were less likely to produce a son when the offspring of the previous year was also a male. We calculated the strength of the effects using the best fitting model, with no intercept and including only the factors year quality and sex of the previous offspring nested within poor years (Table 3). After good years, the calculated probability of producing a male foal was 60%, and after poor years and a

female foal, the probability was close, 58%; however, after poor years and a male foal the probability of producing another male foal was only 24%. We carried out a final test for an effect of mother's age using this model; none was detectable ( $\chi_2 = 0.50$ ,  $df = 2$ ,  $P = 0.78$ ).

#### Juvenile mortality

Of the 215 foals of known sex, 11 were born outside the study herd after their mothers were removed and 1 was removed with its mother before 10 days of age: they were therefore excluded from the analyses of the mortality rates.

Virtually all foal mortality occurred within the first few days of life so we calculated neonatal mortality to 10 days. The overall mortality rate of the foals in the herd was low (21/203 = 10%) and showed some variation across the 15 years (0.0–35%).

Logistic regression revealed a significant interaction between the sex of the foal and year quality at birth, which was entirely due to variations in the mortality rates of males (Table 4). The other variables tested (timing of birth, mother's parity, age and rank at birth, and sex of the offspring reared the previous year) had no effect on foal mortality. Using the most parsimonious model (with an intercept and year quality nested within male foals) we calculated the probability of mortality for juveniles of the two sexes: female foals had the same probability of dying in any year (11%); in contrast, male

**Table 2** Birth sex ratio as a function of mother's parity and age. Data from 1975–1989

	% Males	n
Mother's parity		
Primiparous	48	33
Multiparous	51	182
Mother's age (years)		
2–6	52	100
7–12	48	84
13+	55	31

**Table 3** Logistic regression model of the probability of producing a son, with weighted-least-squares estimates for the parameters. Year quality in the year of conception and sex of the offspring of the previous year (*Sexsib1*) as class variables;  $n = 164$  foals. Model residual ( $\chi_2 = 3.28$ ,  $df = 2$ ,  $P = 0.1940$ )

Source	df	Chi-square	P-value	Parameter estimates
Year quality	1	6.35	0.0117	0.4174
Sexsib1 (Year quality = poor)	1	4.09	0.0432	0.7424

**Table 4** Logistic regression model of the probability of dying in the first 10 days, with weighted-least-squares estimates for the parameters. Year quality at birth and sex of the foal (*Sexf*) as class variables;  $n = 203$  foals. Model residual ( $\chi_2 = 0.00$ ,  $df = 1$ ,  $P = 0.9609$ )

Source	<i>df</i>	Chi-square	<i>P</i> -value	Parameter estimates
Intercept	1	72.61	0.0000	-2.1006
Year quality ( <i>Sexf</i> = female)	1	0.01	0.9051	-0.0389
Year quality ( <i>Sexf</i> = male)	1	8.72	0.0032	-1.0603

foals were less likely to survive in poor years than in good ones (26% versus 4% mortality).

#### Reproductive costs of raising a son

In the section above we tested for one reproductive cost of raising sons, i.e. the probability of mortality of the foals born the year following the rearing of a male. Adult female mortality in this herd was minimal, so we did not test for differential subsequent survival of mothers that reared male versus female offspring. We could, however, evaluate three other potential reproductive costs. The sex of the offspring reared in the previous year had no effect on the probability of foaling the next year (after good years: frequency of foaling = 93.8% after rearing a male versus 94.8% after a female, Fisher exact probability test,  $n_1 = 65$ ,  $n_2 = 58$ ,  $P = 1$ ; after poor years: frequency of foaling = 94.1% versus 83.3%,  $n_1 = 17$ ,  $n_2 = 24$ ,  $P = 0.38$ ).

The condition of mothers did not show any significant trend from conception to birth whatever the sex of the gestated and the suckled offspring (all slopes:  $P > 0.05$ ). The sex of the suckled foal had no significant effect on the  $y$ -intercept of the relationship, in good or in bad years ( $F_{1,296} = 0.04$ ,  $P = 0.848$  and  $F_{1,189} = 0.14$ ,  $P = 0.708$ , respectively). However, in poor years, mothers that gave birth to a son were in better condition than mothers that gave birth to a daughter ( $-0.690 \pm 0.135$  versus  $-0.410 \pm 0.088$ ;  $F_{1,190} = 4.38$ ,  $P = 0.0377$ ,  $r^2 = 0.02$ ). In good years, the condition of mothers bearing a male or a female foal did not differ significantly ( $F_{1,297} = 1.91$ ,  $P = 0.1681$ ).

However, mothers that reared a son in poor years tended to experience an increase in the interbirth interval between their two subsequent offspring compared to those that reared a daughter (median interval = 371.5 versus 361 days; Mann-Whitney  $U$ -test:  $n_1 = 8$ ,  $n_2 = 14$ ,  $U = 29.5$ ,  $0.05 < P < 0.1$ ). An analysis of variance to separate the effects of the sex of the suckled and the gestated offspring on subsequent interbirth interval gave the same trend but was not significant because of very small sample sizes ( $n = 2$  in one class; Kruskal-Wallis analysis of variance:  $H = 4.569$ ,  $df = 3$ ,  $P = 0.206$ ). In good years, the sex of the suckled offspring had no significant effect on the subsequent interbirth interval (median interval = 364 days after rearing a son versus 361 after a daughter;  $n_1 = n_2 = 41$ ,  $z = 1.085$ ,  $P = 0.28$ ).

#### Discussion

There was no significant effect of mother's parity, age or rank, or the timing of conception on the sex ratio at birth in this herd of horses: our results therefore differ from those recently obtained for Asiatic wild asses where young and old females, which may be in poorer condition, produce more female than male offspring (Saltz and Rubenstein 1995). Novellie et al. (1996) found a similar but non-significant trend for young and prime females in one population of Cape mountain zebras. In another population there was no suggestion of an age effect, but dominant mares appear to produce more daughters (Lloyd and Rasa 1989). No bias has been found in feral horses (Berger 1986) or captive Przewalski horses, *Equus ferus przewalskii*, (Mlíkovský 1988).

The birth sex ratio in the Camargue herd did, however, vary in relation to the degree of nutritional stress: mares produced fewer males in years following breeding seasons when they were in poor condition, and this effect was stronger when they had produced a son. These results conform to our prediction based on other studies of mammals (reviewed in Clutton-Brock 1991), which show that variations in birth sex ratios are most often related to resource availability. The significant effect of the sex of the offspring of the previous year on birth sex ratio needs to be interpreted with caution, for the poor years occurred in a block.

The simplest explanation of these results is that differential mortality occurred from the time of conception: if in the four poor years all the mares that failed to foal are assumed to have conceived male offspring (cf. Table 1), then the sex ratio at birth in those years would have been 48%. It has been suggested that males may be more susceptible to prenatal stress due to higher metabolism or other factors arising from sexual selection (see Clutton-Brock et al. 1985). This explanation is consistent with the fact that mothers that gave birth to a male offspring in poor years were in better condition during gestation than those that gave birth to a female.

It is nonetheless possible that, as predicted by Trivers and Willard (1973), maternal adjustment occurred, either pre- or post-zygotic. Prezygotic adjustment could have occurred, through the differential motility or mortality of male and female sperms in relation to the physiological state of the uterus. Post-zygotic adjustment could have occurred through selective resorption

or abortion of male foetuses, with or without re-conception.

If post-zygotic adjustment with re-conception is involved, the interbirth interval should be longer for mares that produced females than males. In fact, interbirth intervals were significantly longer before producing a male offspring than a female (median interval = 371.5 versus 360 days; Mann-Whitney *U*-test:  $n_1 = 14$ ,  $n_2 = 29$ ,  $z = 2.08$ ,  $P < 0.05$ ). The gestation length for male foals is a few days longer than for females (e.g. Berger 1986) but this cannot explain the 12 days difference in the median interval before male offspring. There are several possible explanations, but we have no means of distinguishing them. Adjustment could therefore have resulted either from a prezygotic mechanism or from selective abortion of male foetuses without re-conception in that year.

Virtually all the juvenile mortality in these horses occurred in the first ten days of life (as in feral horses: Berger 1986; and thoroughbreds: Platt 1978). The mortality rate of female foals was unaffected by year quality, but male foals were much more likely to die in poor years than in good ones. In contrast, mother's parity, age or rank, and the timing of birth had no significant effects on foal mortality. Year quality could therefore have been used by the mares as a predictor of sex-specific offspring survival, provided that a poor year tends to be followed by another.

It has been suggested that in some circumstances a mother should terminate her investment in a male offspring (Trivers and Willard 1973). However it is more likely that the higher mortality of male offspring observed in this study was simply due to their being weaker at birth: of the 11 foals that died in poor years, 1 male was trampled by stallions and 1 female abandoned by its mother; 2 other males drowned, 1 female was born weak, 1 female never emerged from the placenta and the remainder 5 (4 males/1 female) were found dead (for unknown reasons).

There was a suggestion that the costs of rearing male offspring exceeded those of rearing females in this study. The sex of the offspring reared in the previous year had no effect on the probability of foaling the next year, or on the probability of mortality of the subsequent offspring; and the condition of the mothers from conception to birth was independent of the sex of the gestated and the suckled offspring. However, mares that reared a son in poor years tended to experience an increase in the interbirth interval between their two subsequent offspring compared to those that reared a daughter.

Female horses have unusually complex patterns of reproduction, and suckle a foal while gestating another, so it is therefore perhaps not surprising that clearcut differences were not found in this species. In addition, horses only show a slight sexual dimorphism, and it is possible that our index was too crude to monitor small-scale changes in the condition of mares. Mammals where sons have been found to entail greater reproductive costs are highly dimorphic, and most of the maternal care is

completed before conceiving another offspring (e.g. red deer, *Cervus elaphus*: Clutton-Brock et al. 1981; bighorn sheep, *Ovis canadensis*: Bérubé et al. 1996).

These results therefore show that birth sex ratio and differential juvenile mortality in these horses were related to environmental conditions. This could be due to differential susceptibility of males to environmental stresses pre- and post-natal; but as in a study of yellow baboons, *Papio cynocephalus* (Wasser and Norton 1993), these results are also consistent with adjustment of the birth sex ratio to maximise inclusive fitness (Trivers and Willard 1973), since there were sex-differences in variance in offspring survival, which is one of the largest components of variance in offspring lifetime reproductive success (Clutton-Brock 1988).

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## References

- Bassett PA (1978) The vegetation of a Camargue pasture. *J Ecol* 66:803–827
- Berger J (1986) Wild horses of the Great Basin: social competition and population size. University of Chicago Press, Chicago
- Bérubé CH, Festa-Bianchet M, Jorgenson JT (1996) Reproductive costs of sons and daughters in Rocky Mountain bighorn sheep. *Behav Ecol* 7:60–68
- Clark AB (1978) Sex ratio and local resource competition in a prosimian primate. *Science* 201:163–165
- Clutton-Brock TH (ed) (1988) Reproductive success. University of Chicago Press, Chicago
- Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton, New Jersey
- Clutton-Brock TH, Iason GR (1986) Sex ratio variation in mammals. *Q Rev Biol* 61:339–374
- Clutton-Brock TH, Albon SD, Guinness FE (1981) Parental investment in male and female offspring in polygynous mammals. *Nature* 289:487–489
- Clutton-Brock TH, Albon SD, Guinness FE (1985) Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* 313:131–133
- Duncan P (1992) Horses and grasses: the nutritional ecology of equids and their impact on the Camargue. Springer, Berlin Heidelberg, New York
- Duncan P, Harvey PH, Wells SM (1984) On lactation and associated behaviour in a natural herd of horses. *Anim Behav* 32:255–263
- Feh C (1990) Long-term paternity data in relation to different aspects of rank for Camargue stallions, *Equus caballus*. *Anim Behav* 40:995–996
- Ginther OJ (1979) Reproductive biology of the mare. McNaughton and Gunn, Ann Arbor
- Henneke DR, Potter GD, Kreider JL, Yeates BF (1983) Relationship between condition score, physical measurements and body fat percentages in mares. *Equine Vet J* 15:371–372
- Hintz HF, Hintz RL, van Vleck LD (1979) Growth rate of thoroughbreds. Effects of age of dam, year and month of birth, and sex of foal. *J Anim Sci* 48:480–487
- Klingel H (1974) A comparison of the social behaviour of the Equidae. In: Geist V, Walther F (eds) The behaviour of ungu-

- lates and its relation to management. IUCN, Morges, Switzerland, pp 124-132
- Lloyd PH, Rasa OAE (1989) Status, reproductive success and fitness in Cape mountain zebra (*Equus zebra zebra*). *Behav Ecol Sociobiol* 25:411-420
- Maynard Smith J (1980) A new theory of sexual investment. *Behav Ecol Sociobiol* 7:247-251
- Mlikovský J (1988) Secondary sex ratio in the Przewalski horse *Equus przewalskii* (Mammalia: Equidae). *Z Säugetierk* 53:92-101
- Monard AM, Duncan P, Boy V (1996) The proximate mechanisms of natal dispersal in female horses. *Behaviour* 133:1095-1124
- Novellie PA, Miller PS, Lloyd PH (1996) The use of VORTEX simulation models in a long term programme of re-introduction of an endangered large mammal, the Cape mountain zebra (*Equus zebra zebra*). In: Clobert J, Duncan P, Danchin E (eds) *The ecology and conservation of spatially structured populations*. *Acta Oecol special issue* 17:657-671
- Platt H (1978) A survey of perinatal mortality in the thoroughbred. Animal Health Trust, Newmarket
- Ridgill SC, Fox AD (1990) Hard weather movements of waterfowl in the western palaeartic. (IWRB Special Publication no 13). Wetlands International, Slimbridge
- Saltz D, Rubenstein DI (1995) Population dynamics of a reintroduced asiatic wild ass (*Equus hemionus*) herd. *Ecol Appl* 5:327-335
- SAS Institute (1989) SAS/STAT user's guide, version 6, 4th edn. SAS Institute, Cary
- Schaik CP van, Hrdy SB (1991) Intensity of local resource competition shapes the relationship between maternal rank and sex ratios at birth in cercopithecine primates. *Am Nat* 138:1555-1562
- Silk J (1983) Local resource competition and facultative adjustment of sex ratios in relation to competitive abilities. *Am Nat* 121:56-66
- Smuts GL (1976) Population characteristics of Burchell's zebra (*Equus burchelli antiquorum*, H Smith, 1841) in the Kruger National Park. *S Afr J Wildl Res* 6:99-112
- Trivers RL, Willard DE (1973) Natural selection of parental ability to vary the sex ratio of offspring. *Science* 179:90-92
- Waring GH (1983) Horse behavior: the behavioral traits and adaptations of domestic and wild horses, including ponies. Noyes, Park Ridge
- Wasser SK, Norton G (1993) Baboons adjust secondary sex ratio in response to predictors of sex-specific offspring survival. *Behav Ecol Sociobiol* 32:273-281
- Wells SM, Goldschmidt-Rothschild B von (1979) Social behaviour and relationships in a herd of Camargue horses. *Z Tierpsychol* 49:363-380
- Welsh DA (1975) Population, behavioural, and grazing ecology of the horses of Sable Island, Nova Scotia. MSc thesis, Dalhousie University, Canada

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