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Birth sex ratios relate to mare condition at conception in Kaimanawa horses

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Several hypotheses have been proposed to explain variation in birth sex ratios, based on the premise that variation is expected when the profitability of raising sons and daughters varies between individual parents. We tested the Trivers-Willard hypothesis that mothers in better condition produce relatively more sons and that mothers in poorer condition produce relatively more daughters when male reproductive success is more variable. We examined birth sex ratios in relation to mare body condition at conception in horses in which male reproductive success is differentially helped by slight advantages in condition. Horses meet the assumptions of the Trivers-Willard hypothesis better than many species on which it has been tested and in which sex ratio biases are not confounded by sexual size dimorphism such that one sex is more likely to die in utero in females in poor condition. Mares that had a female foal were in poorer condition at conception than those that had a male foal, and mares that had foals of different sexes in different years were in significantly poorer condition when they conceived their female foal. There was no relationship between offspring sex and mid-gestation condition, and there was no difference in foaling rates in relation to body condition at conception. Consequently, sex ratio deviations are not explained by fetal loss in utero. Furthermore, differential fetal loss of the less viable sex cannot explain the greater proportion of males produced by mares in better condition. Therefore, our results suggest that sex ratio modification occurs at conception in wild horses. *Key words:* birth sex ratios, Equus caballus, fetal loss, maternal condition, Trivers-Willard hypothesis, wild horses. *[Behav Ecol 10:472–475 (1999)]*

Sex ratios at birth and hatching can vary (Clutton-Brock, 1985; Clutton-Brock et al., 1986; Clutton-Brock and Iason, 1986; Frank, 1990; Hardy, 1997). Adaptive theories predict variation in birth sex ratio when the profitability of raising sons and daughters varies between individual parents (Trivers and Willard, 1973). Large sex ratio variations were recently reported in Seychelles warbler eggs, indicating differential conception of male and female offspring in relation to offspring profitability (Komdeur et al., 1997). In mammals, although variations in birth sex ratios tend to be relatively small and some estimates have been based on inadequate evidence (Festa-Bianchet, 1996), some studies have shown significant variation (Clutton-Brock and Iason, 1986).

The Trivers-Willard model suggests that where one sex has more variable reproductive success, such as males in polygynous species, mothers in good condition will be benefited by producing more of that sex, whereas mothers in poor condition would be benefited by producing more of the reproductively stable sex (Trivers and Willard, 1973). The hypothesis is appropriate for species with a small litter size and depends on three premises (Trivers and Willard, 1973): (1) that the condition of the young at the end of parental investment will tend to be correlated with the condition of the mother during parental investment; (2) that these differences in condition tend to endure into adulthood; and (3) that adult males will be differentially helped in reproductive success by slight advantages in condition, such as through intense male–male competition in polygynous species.

Wild horses meet these assumptions better than most mammal species on which the hypothesis has been tested previously. Horse litter size is fixed at one (Platt, 1978). Differential investment in male and female offspring has been reported (Berger, 1986; Duncan et al., 1984), and this varies with maternal condition: mares in good condition invest more in sons, whereas mares in poor condition invest more in daughters (Cameron and Linklater, submitted). There is a correlation between maternal rank (which is related to condition, as dominant mares have access to better resources; Duncan, 1992) and reproductive success in both males (Feh, 1990) and females (Duncan, 1992), suggesting a correlation between female condition and offspring condition and reproductive success as adults. However, because male reproductive success is more variable, a mother's rank has a greater effect on her son than on her daughter. In some other species, one sex may be easier to invest in than the other. For example, where sons disperse and daughters are philopatric, it may be easier to influence the reproductive success of daughters for relatively little extra investment. This is not the case in horses, where both male and female offspring disperse, and so there can be no direct inheritance of social rank (Berger, 1986; Rutberg and Keiper, 1993). In addition, sexual size dimorphism at birth is minimal (Duncan, 1992), so males are not markedly more costly to raise in utero due to accelerated growth rates alone, which has been a frequently cited reason that mothers in poor condition lose more male offspring in other species (Clutton-Brock, 1991).

Previous studies have examined offspring sex ratios in mammals in relation to indices of condition such as food availability or diet (e.g., Monard et al., 1997; Smith et al., 1996), maternal ranking (e.g., Cassinello and Gomendio, 1996; Clutton-Brock et al., 1984; Green and Rothstein, 1991), whether mothers were primiparous or multiparous (e.g., Cassinello and Gomendio, 1996), reproductive success in the previous year (e.g., Green and Rothstein, 1991; Rutberg, 1986), interval since last offspring (e.g., Wiley and Clapham, 1993), or maternal body condition at slaughter when fetuses are mature enough to be sexed (e.g., Reimars and Lenvik, 1997; Wauters et al., 1995). In Camargue horses, Monard et al. (1997) found

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that sex ratios were female biased in years following a season of poor food availability, during which mares were in poorer body condition. However, they were unable to determine if differences were due to differential conception or to differential fetal loss during gestation. Estimates of female body condition around (Kojola and Eloranta, 1989) or before (Moses et al., 1995) conception provide more appropriate estimates at the time when sex ratio adjustment can occur (Krackow, 1995) than at times that are more observable for researchers, but when adjustment does not necessarily occur.

We aimed to determine if birth sex ratios vary according to the predictions of the Trivers-Willard hypothesis in relation to condition at conception both within and between individual mares. We examined differences in foaling rates of mares in different condition to determine if sex ratio variation is likely due to differential loss of offspring or to differences in conception sex ratio. Furthermore, we investigated variation in sex ratio in relation to the previously used indices of whether mares are primiparous or multiparous, previous year's foaling success, and mid-gestation condition.

METHODS

Feral horses (*Equus caballus*), known locally as Kaimanawa horses, inhabit the Kaimanawa mountains and surrounding plateaus and valleys of central North Island, New Zealand. Since August 1994 we have been studying a population of approximately 400 of these horses which inhabit the Moawhango River basin and surrounding plateau. Individual horses were reliably identifiable by either freeze brands on their rumps or by natural markings.

Body condition scores were estimated by visual body fat distribution based on an 11-point scale from 0–5 with 0.5 gradations (Carroll and Huntingdon, 1988; Huntingdon and Cleland, 1992; Rudman and Keiper, 1991) with the aid of 10–15× binoculars or a 15–60× telescope whenever horses were sighted, provided visibility was good. Scores of 0 were very poor and scores of 5 were obese. Interobserver reliability was high ($r = .91$). In horses, body condition scores correlate with body fat percentage ($r = .81$; Henneke et al., 1983).

We calculated body condition at conception for Kaimanawa mares by backdating from the date of foaling (accurate to ±5 days) by the average gestation length±1 SD (336±10 days; Kiltie, 1982) and taking the mode of visual body condition scores during this period for foals born in 1995, 1996, and 1997, and at mid-gestation (168±10 days) for foals born in 1995 and 1996. All mares used in the analysis were scored at least twice during these 20-day periods, and mares were only scored once on any one day. We also calculated modal body condition scores for mares in the month before birth, and for foals in their 12th month to determine if female condition during investment was reflected by foal condition near the end of the period of investment.

Body condition scores at conception approximated a normal distribution, with the modal scores of most mares being 2.5 and a range of 1 to 4. Thirty-three mares foaled once, 30 foaled twice, and 14 foaled three times between 1994 and 1997.

We classified mares as primiparous if they had not foaled before and were known to be too young (≤ 2 years) to have foaled prior to the study ($n = 22$). Mares were classified as multiparous only if they were known to have foaled previously ($n = 103$; unknown, $n = 10$). We also classified mares in relation to their previous year's reproductive success (no foal or lost foal $n = 67$; successfully raised foal to 6 months, $n = 67$; unknown, $n = 1$).

We recorded the sex of every foal born to a mare within the focal population in the foaling season (September to February) starting in 1995 ($n = 42$), 1996 ($n = 55$), and 1997 ($n = 38$) by sighting genitalia, which are visible in both sexes from birth.

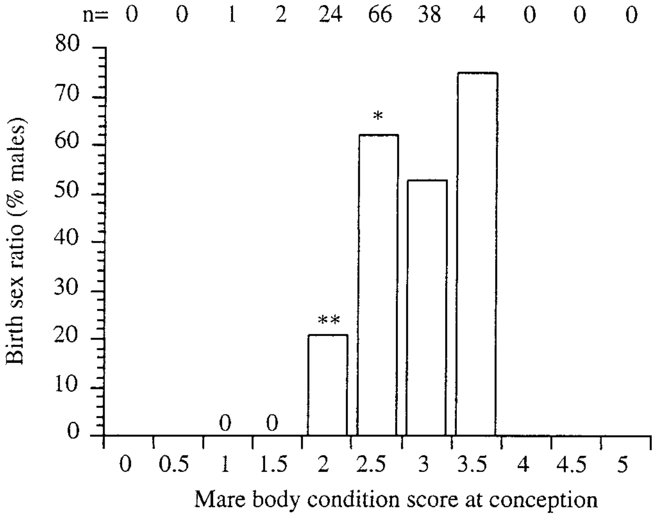

Figure 1
Birth sex ratios in relation to condition at conception in Kaimanawa horses. Note that no mares of condition <1 at conception time bore live foals and that no mare scored >3.5 at conception. Asterisks indicate significant differences from an expectation of parity: *$p < .05$, **$p < .01$.

To determine if foaling rates were different between mares of different condition at conception, we recorded the condition of all mares during the mean conception date±1 SD (15 November–16 January 1994–95 and 1995–96) and recorded which of these mares foaled in the subsequent season.

The results of statistical tests presented are two-tailed.

RESULTS

There was a significant difference between the condition at conception of mares who had a female foal and mares who had a male foal (Mann-Whitney U test, $U = 2794$, $N_1 = 69$, $N_2 = 66$, $p < .05$). Mare condition at conception was a significant predictor of offspring sex (logistic regression, $\chi^2 = 7.89$, df = 1, $p < .01$; Figure 1). Furthermore, we compared the condition at conception of mares that had foals of different sexes and found that mares were in significantly poorer condition when they conceived their female foal (Wilcoxon signed-ranks paired test, $Z = 2.23$, $N = 25$, $p < .05$).

The sex ratio varied significantly from parity in both directions. Although differences were not significant for mares of condition 1, 1.5, 3, and 3.5, mares of condition 2 gave birth to significantly fewer sons than expected (binomial test, $p < .01$) and mares of condition 2.5 gave birth to significantly more sons than expected (binomial test, $p < .05$).

There was no difference in birth dates throughout the season for male or female offspring (Mean birth date = Mann-Whitney U test, $U = 2205$, $N_1 = 69$, $N_2 = 66$, ns). There was no significant variation in sex ratio between primiparous and multiparous mares, whether a mare had foaled in the previous year or in the year the foal was born in (Table 1).

Although mare condition at conception was correlated with mare condition at mid-gestation ($r_s = .36$, $n = 72$, $p < .05$), there was no difference in mare condition at mid-gestation between mothers who had a male or female foal (Mann-Whitney U test, $U = 777$, $N_1 = 41$, $N_2 = 36$, ns), and mare condition at mid-gestation did not predict foal sex (logistic regression, $\chi^2 = 0.31$, df = 1, ns). The correlation was stronger

Table 1

Variation in sex ratio in relation to mare experience, previous year's foaling success, and condition at mid-gestation

Category[a]	% Male	*n*	Unity[b]	*G* test[c]
Experience				ns
Primiparous	50	22	ns	
Multiparous	50	103	ns	
Previous year				ns
Foal	51	67	ns	
No foal	49	67	ns	
Year				ns
1995	55	42	ns	
1996	55	55	ns	
1997	42	38	ns	

[a] Ten mares were of unknown parity, and previous year's reproduction was unknown in one case.

[b] Deviation from an expectation of unity is calculated from a binomial distribution.

[c] *G* test with Williams correction (Sokal and Rohlf, 1981).

between condition at conception and condition during the month before birth ($r_s = .64$, $n = 80$, $p < .001$), although mare condition before foal birth did not predict foal sex (logistic regression, $\chi^2 = 1.11$, df = 1, ns). There was also a correlation between mare condition before birth and foal condition as yearlings ($r_s = .62$, $n = 72$, $p < .05$).

There was no significant difference in foaling rates with condition at conception (logistic regression, $\chi^2 = 0.34$, df = 1, ns). About 30% of all mares did not foal.

In mares that foaled in subsequent years, there was a no difference in time between birth of the current foal and the conception of male or female foals (Mann-Whitney *U* test, $U = 514$, $N_1 = 37$, $N_2 = 35$, ns), though there was a tendency for males to be conceived after a longer period of time.

DISCUSSION

Our study confirms the applicability of Kaimanawa horses as an ideal test of the Trivers-Willard hypothesis. Mares only ever had one foal per breeding attempt, and there was a correlation between mare body condition during investment and foal condition as yearlings when maternal investment was ending. Although we do not show that these advantages endure into adulthood, previous studies show increased reproductive success in the offspring of dominant mares (Duncan, 1992; Feh, 1990). Theoretically, males will be differentially helped by condition advantages in a species as highly polygynous as the horse.

Our results strongly support the predictions of the Trivers-Willard hypothesis. In the Kaimanawa horse population, mares in poor condition at conception gave birth to predominantly female foals, as did Camargue mares in the year following a season of poor food availability (Monard et al., 1997). There was no significant difference in foaling rates in relation to condition at conception, and about 30% of all mares did not produce a foal. Our 70% live foal rate is similar to rates found in other studies of both domestic (50–80%; Rossdale and Ricketts, 1980) and wild (45–74%; Keiper, 1979; Keiper and Houpt, 1984) horses. Some unrecorded loss of neonates may also have occurred, as neonatal mortality can be high in horses (Berger, 1986; Duncan, 1992; Waring, 1983). However, live foal rates were similar regardless of condition at conception, and death of neonates is likely to be similar irrespective of the mother's earlier condition. Therefore, it seems unlikely that the birth sex ratios we report are due to differential death of fetuses or neonates by mares in poorer condition. In addition, those mares who had a male foal in one year and a female in another were in significantly poorer condition when they conceived their female foal.

Furthermore, mares in better condition produced more male foals than expected from an assumption of parity. Where sex ratios differ significantly from parity in both directions, it is unlikely that the difference is due solely to differential loss of less viable or more costly fetuses—usually males in mammalian species (Clutton-Brock, 1991). For sex ratios that differ from parity in both directions to be explained by differential loss of less viable or more costly fetuses, daughters would have to be less viable in good-condition mares and sons less viable in poor-condition mares (Clutton-Brock, 1991). Alternatively, mechanisms that favor the differential conception of males or females have been postulated (Krackow, 1995; e.g., timing of insemination, Guerrero, 1974; Paul and Kuester, 1987; embryonic mortality, Huck et al., 1988).

We found no difference in sex ratio between multiparous and primiparous mares or whether a mare had foaled in the previous year. Furthermore, by mid-gestation maternal condition was no longer a predictor of offspring sex ratio, supporting the premise that sex ratios vary due to differential conception of male and female offspring. Indeed, although condition during gestation has been frequently used to examine sex ratio variation (e.g., supporting Trivers-Willard: Burke and Birch, 1995; Kucera, 1991; Rutberg, 1986; Wauters et al., 1995; not supporting Trivers-Willard: Hewison and Gaillard, 1996; Reimars and Lenvik, 1997), such studies must assume that either sex ratios are adjusted during gestation or that condition has not changed significantly since conception. In species with long gestation, such as horses (11 months), condition may change significantly during gestation. If males do cost more than females in utero, as is suggested for several sexually dimorphic species (Clutton-Brock, 1991), then mothers carrying male offspring may lose more weight during pregnancy than mothers carrying female offspring. Measures of body condition at or around conception (e.g., Kojola and Eloranta, 1989; Moses et al., 1995) provide a more accurate test of the Trivers-Willard hypothesis than measures taken during gestation if, as our data suggest, biases are caused by differential conception of males and females and not by differential loss of fetuses during gestation.

Previous studies on mammals have documented variation in sex ratio in relation to female weight around the time of conception, in line with the prediction that females in good condition produce more male offspring (reindeer: Kojola and Eloranta, 1989; bushy-tailed woodrats: Moses et al., 1995), suggesting differential conception may be occurring. In Kaimanawa horses, the birth sex ratio differs from parity in both directions depending on mare condition at conception, and variations in the birth sex ratio are too large to be accounted for by differential fetal loss alone. In addition, there is no variation in sex ratio in relation to condition during gestation. Therefore, our data suggest that the sex ratio variation occurs near to conception and before sexual differentiation.

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REFERENCES

Berger J, 1986. Wild horses of the Great Basin. Chicago: University of Chicago Press.

Burke RL, Birch JM, 1995. White-tailed deer vary offspring sex-ratio according to maternal condition and age. Ecol Res 10:351–357.

Carroll CL, Huntingdon PJ, 1988. Body condition scoring and weight estimation in horses. Equine Vet J 20:41–45.

Cassinello J, Gomendio M, 1996. Adaptive variation in litter size and sex ratio at birth in a sexually dimorphic ungulate. Proc R Soc Lond B 263:1461–1466.

Clutton-Brock TH, 1985. Birth sex ratios and the reproductive success of sons and daughters. In: Evolution: essays in honour of John Maynard Smith (Greenwood PJ, Harvey PH, Slatkin M, eds). Cambridge: Cambridge University Press; 221–235.

Clutton-Brock TH, 1991. The evolution of parental care. Princeton, New Jersey: Princeton University Press.

Clutton-Brock TH, Albon SD, Guinness FE, 1984. Maternal dominance, breeding success and birth sex ratios in red deer. Nature 308:358–360.

Clutton-Brock TH, Albon SD, Guinness FE, 1986. Great expectations: dominance, breeding success and offspring sex ratios in red deer. Anim Behav 34:460–471.

Clutton-Brock TH, Iason GR, 1986. Sex ratio variation in mammals. Q Rev Biol 61:339–374.

Duncan P, 1992. Horses and grasses: the nutritional ecology of equids and their impact on the Camargue. New York: Springer-Verlag.

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 rank aspects for Camargue stallions. Anim Behav 40:995–996.

Festa-Bianchet M, 1996. Offspring sex ratio studies of mammals: does publication depend upon the quality of the research or the direction of the results? Ecoscience 3:42–44.

Frank SA, 1990. Sex allocation theory for birds and mammals. Annu Rev Ecol Syst 21:13–55.

Green WCH, Rothstein A, 1991. Sex bias or equal oppurtunity? Patterns of maternal investment in bison. Behav Ecol Sociobiol 29: 373–384.

Guerrero R, 1974. Association of the type and time of insemination within the menstrual cycle with the human sex ratio at birth. N Engl J Med 291:1056–1059.

Hardy ICW, 1997. Possible factors influencing vertebrate sex ratios: an introductory overview. Appl Anim Behav Sci 51:217–241.

Henneke DR, Potter GD, Kreider JL, Yeates BF, 1983. Relationship between condition score, physical measurements and body fat percentage in mares. Equine Vet J 15:371–372.

Hewison AJM, Gaillard JM, 1996. Birth-sex ratios and local resource competition in roe deer, *Capreolus capreolus*. Behav Ecol 7:461–464.

Huck UW, Lisk RD, Miller KS, Bethel A, 1988. Progesteron levels and socially induced implantation failure and fetal resorption in golden hamsters (*Mesocrietus auratus*). Physiol Behav 44:321–326.

Huntingdon P, Cleland F, 1992. Horse Sense: The Australian guide to horse husbandry. Melbourne: Agmedia.

Keiper RR, 1979. Population dynamics of feral ponies. In: Symposium on the ecology and behavior of wild and feral equids (Denniston RH, ed). Laramie: University of Wyoming; 175–183.

Keiper RR, Houpt K, 1984. Reproduction in feral horses: an eight-year study. Am J Vet Res 45:991–995.

Kiltie RA, 1982. Intraspecific variation in the mammalian gestation period. J Mammal 63:646–652.

Kojola I, Eloranta E, 1989. Influences of maternal body weight, age, and parity on sex ratio in semidomesticated reindeer (*Rangifer t. tarandus*). Evolution 43:1331–1336.

Komdeur J, Daan S, Tinbergen J, Mateman C, 1997. Extreme adaptive modification in sex ratio of the Seychelles warbler's eggs. Nature 385:522–525.

Krackow S, 1995. Potential mechanisms for sex ratio adjustment in mammals and birds. Biol Rev 70:225–241.

Kucera TE, 1991. Adaptive variation in sex ratios of offspring in nutritionally stressed mule deer. J Mammal 72:745–749.

Monard A-M, Duncan P, Fritz H, Feh C, 1997. Variations in the birth sex ratio and neonatal mortality in a natural herd of horses. Behav Ecol Sociobiol 41:243–249.

Moses RA, Hickling GJ, Millar JS, 1995. Variation in sex ratios of offspring in wild bushy-tailed woodrats. J Mammal 76:1047–1055.

Paul A, Kuester J, 1987. Sex ratio adjustment in a seasonally breeding primate species: evidence from a Barbary macaque population at Affenberg Salem. Ethology 74:117–132.

Platt H, 1978. A survey of perinatal mortality and disorders in the thoroughbred. Newmarket: The Animal Health Trust.

Reimars E, Lenvik D, 1997. Fetal sex ratio in relation to maternal mass and age in reindeer. Can J Zool 75:648–650.

Rossdale PD, Ricketts SW, 1980. Equine stud farm medicine, 2nd ed. London: Baillière Tindall.

Rudman R, Keiper RR, 1991. The body condition of feral ponies on Assateague Island. Equine Vet J 23:453–456.

Rutberg AT, 1986. Lactation and fetal sex ratios in American bison. Am Nat 127:89–94.

Rutberg AT, Keiper RR, 1993. Proximate causes of natal dispersal in feral ponies: some sex differences. Anim Behav 46:969–975.

Smith BL, Robbins RL, Anderson SH, 1996. Adaptive sex ratios: another example? J Mammal 77:818–825.

Sokal RR, Rohlf FJ, 1981. Biometry. The principles and practice of statistics in biological research, 2nd ed. New York: W. H. Freeman.

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. Park Ridge, New Jersey: Noyes Publications.

Wauters LA, de Crombrugghe SA, Nour N, Matthysen E, 1995. Do female roe deer in good condition produce more sons than daughters? Behav Ecol Sociobiol 37:189–193.

Wiley DN, Clapham PJ, 1993. Does maternal condition affect the sex ratio of offspring in humpback whales? Anim Behav 46:321–324.