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Foetal sex ratios in wild reindeer *Rangifer tarandus* in relation to maternal condition and age

Eigil Reimers

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Sex and total weight were recorded in 215 wild reindeer *Rangifer tarandus tarandus* foetuses from six ranges evaluated as good, medium, and poor based on maternal weights. The proportions of males per 100 females in the good, medium and poor ranges were 76, 112 and 100, respectively, and 94 overall. None of these ratios were statistically different from a 50:50 sex distribution. Examination of individual year and weight classes within areas revealed no difference in foetus sex ratio from a 50:50 ratio. Male and female foetus mean weight differences varied between 28 and 216 g within areas when measured in February and March. None of these differences were significant. Male foetus weights were significantly higher than female weights in April in a pooled sample from the good ranges. Although the sample size is too small for a conclusive statement, the data do not support the Trivers & Willard hypothesis that females should produce more male offspring when resources are abundant.

Key words: foetal sex ratio, Rangifer tarandus, reindeer, Trivers & Willard hypothesis

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Trivers & Willard (1973) predicted that under certain conditions females could adjust the sex ratios of their offspring to maximise their own genetic contribution to future generations. They used caribou *Rangifer* as a hypothetical model; a model that fits polygynous and sexually dimorphic species and which was driven by differences in physical condition. According to the hypothesis, adult males will be differentially aided in reproductive success (compared to adult females) by slight advantages in condition. Slight advantages in condition should have disproportionate effects on male reproductive success compared to the effect on female reproductive success because males compete to inseminate females. The prenatal ratio of males to females should decline as maternal condition declines and increase when maternal condition improves. The mechanism by which differential prenatal mortality may occur was not presented.

In a recent paper, Leimar (1996) argues against the Trivers & Willard (1973) hypothesis on the basis of an apparently improper analysis of variation in reproductive values. Based upon state-dependent life history theory, Leimar (1996) showed that high-quality females should prefer offspring of the sex whose reproductive value is most strongly influenced by maternal care. When offspring quality is strongly determined by their mother's quality, but not influenced by their father's quality, high-quality females may have higher reproductive value than high-quality males. In such cases, high-quality females should

Table 1. Maternal size (mean dressed weight + foetus weight) and prenatal sex-ratio for six reindeer herds in good, medium and poor ranges.

Herd	Year	Range quality	Maternal size (kg ± SD)	Prenatal sex ratio		Binomial test		χ^2-test
				♂	♀	P	χ^2	P
Forelhogna	1984[1]	Good	46.4 ± 5.5 (22)[2]	8	14	0.28		
Knutshø	1984[1]	-	42.4 ± 2.7 (23)[2]	11	12	1.00		
North and South Ottadalen	1967-72	-	42.7 ± 7.1 (13)[2]	6	7	1.00		
Subtotal		Good		25	33	0.36	0.67	0.71
Rondane North	1972-73	Medium	33.9 ± 3.3 (17)[2]	9	8	1.00		
Snøhetta	1957-64	Poor	30.0 ± 3.3 (31)[2]	13	16	0.71		
Hardangervidda	1957-58	-	31.1 ± 3.4 (22)[2]	10	10	1.00		
	1970-73	-	29.4 ± 3.9 (37)[2]	20	11	0.15		
	1983[1]	-	26.0 ± 3.0 (60)[2]	27	33	0.52		
Subtotal		Poor		70	70	1.00	2.48	0.29
Total				104	111	0.68	5.12	0.65

[1] Data from Skogland (1986) and T. Skogland & E. Reimers (unpubl. data).

[2] Sample size.

prefer daughters and low-quality females should prefer sons.

Although the logic of the argument by Trivers & Willard (1973) seems to have been generally accepted (Charnov 1982, Clutton-Brock & Albon 1982, Frank 1990), tests of their prediction on a number of polygynous and sexually dimorphic species have resulted in male-biased, female-biased and unbiased sex ratios in relation to maternal condition or age (Clutton-Brock & Iason 1986, Hoefs & Nowlan 1994, Kojola & Helle 1994). Because Trivers & Willard (1973) did not predict any quantitative difference in the foetal sex ratio, just its direction, a critical test of the hypothesis requires a large number of foetuses from mothers in good vs poor condition. This requirement is rarely met.

This paper presents data on prenatal sex ratios in wild reindeer *Rangifer tarandus tarandus* from good, medium, and poor ranges. Ranges were evaluated based on relative maternal weights.

Material and methods

Data include 215 female reindeer killed under various sampling programs in six wild reindeer areas in southern Norway (Table 1). The data from Forelhogna and Knutshø in 1984 and Hardangervidda 1983 are from Skogland (1986). Sampling occurred during winter from November through May. Free-ranging female *Rangifer* lose body weight through winter (Reimers 1983). Some of this maternal carcass weight loss is transferred to the growth of the foetus. To minimise the effect of different sampling dates on the body weight of the females, the mean maternal weights in the various areas include the maternal carcass weight and the weight of the foetus. Age was determined from tooth development or tooth wear (animals sampled in 1957-1958) or annuli in the incisor teeth cementum (Reimers & Nordby 1968). Deviations from 1:1 foetus sex ratios were tested by binomial tests, and the differences between

Table 2. χ^2-tests of foetus sex according to three age classes, 1-3, 4-9 and ≥10 years, and range quality of wild reindeer. Cells in the ≥10 age interval in the good range quality areas were pooled with the 4-9 age class when χ^2 was tested.

	Range quality							
	Good		Medium		Poor		Total sample	
Age class at breeding	♂	♀	♂	♀	♂	♀	♂	♀
1-3	10	11	5	5	21	18	36	34
4-9	14	21	4	3	45	50	63	74
≥10	1	1			4	2	5	3
Sum	25	33	9	8	70	70	104	111
χ^2	0.25		0.08		1.16		1.21	
Degrees of freedom	1		1		2		2	
Significance level (P)	0.62		0.77		0.56		0.55	

Table 3. χ^2-tests of foetus sex according to maternal size (mean dressed weight + foetus weight in kg) and range quality. Cells with two or less observations were pooled with the next higher weight interval when χ^2 was tested.

	Range quality							
	Good		Medium		Poor		Total sample	
Maternal size[1]	♂	♀	♂	♀	♂	♀	♂	♀
15					2	1	2	1
20					12	11	12	11
25	0	1	2	1	33	33	35	35
30	0	1	5	3	21	20	26	24
35	2	8	2	4	2	5	6	17
40	12	13					12	13
45+	11	10					11	10
Sum	25	33	9	8	70	70	104	111
χ^2	4.34		1.49		1.46		5.32	
Degrees of freedom	2		1		3		5	
Significance level (P)	0.11		0.22		0.69		0.38	

[1] Lower weight interval, e.g. in the poor area the dressed weight + weight of foetus was within a weight interval of 15-19.9 kg for three animals.

empirical distributions were tested by χ^2-tests. Logistic regression analyses (Steinberg & Colla 1994) was used to test the hypothesis that foetal sex was influenced by: female age at conception, area, female weight, area quality, year of conception, female cohort. A forward stepping procedure was used with the dependent variable foetal sex coded as 1 or 2. The independent variables were either categorical (area and area quality) or continuous (age, weight, year and cohort). Criterion for entrance of independent variables into the model was $P \leq 0.05$. ANOVA was used to test weight differences.

Results

The proportions of males produced by females in the good (N = 58), medium (N = 17) and poor ranges (N=140) were 76, 112 and 100 males to 100 females, respectively. In the total sample (N = 215) the foetus sex proportion was 94 males to 100 females (see Table 1). None of the above-mentioned sex ratios differed significantly from a 50:50 ratio. Examination of individual year classes (Table 2) or weight classes (Table 3) revealed no significant difference in foetus sex proportion from 50:50. A forward, stepwise logistic regression (see Material and methods) showed that none of the independent variables were significant predictors of foetal sex ($\chi^2 = 3.72$, df = 8, P = 0.81). T-ratios and P-values for independent variables were: female age: t = 0.37, P = 0.71; area: t = -0.85, P = 0.39; female weight: t = 1.36; P = 0.18; area quality: t = 0.81, P = 0.42; female cohort: t = -0.53, P = 0.60; female age × female weight: t = -0.54, P = 0.59; female weight × area quality: t = -1.19, P = 0.24; area × area quality: t = 1.06, P = 0.29.

Male and female foetus mean weight differences varied between 28 and 216 g within areas when measured in February and March (Table 4). None of these differences were significant. Male foetus weights were significantly higher than female weights in April in a pooled sample from the good areas.

Table 4. Male and female foetus weights according to area and month.

		Foetus weight (g ± SD)			
Area	Month	♂	♀	F	P
Forelhogna and Knutshø	February	1036 ± 690 (10)[1]	947 ± 238 (6)[1]	10.09	0.77
North and South Ottadalen	March	1846 ± 505 (7)[1]	1642 ± 433 (10)[1]	0.80	0.39
	April	4388 ± 1261 (8)[1]	3389 ± 679 (17)[1]	6.73	0.016
Rondane North	February	421 ± 190 (4)[1]	449 ± 220 (4)[1]	0.04	0.85
	April	3300 (1)[1]	2950 ± 666 (4)[1]	0.22	0.67
Hardangervidda and Snøhetta	February	545 ± 202 (22)[1]	601 ± 329 (22)[1]	0.47	0.50
	March	1517 ± 332 (11)[1]	1414 ± 400 (21)[1]	0.53	0.47
	April	2567 ± 533 (24)[1]	2351 ± 486 (20)[1]	1.94	0.17

[1] Sample Size.

Discussion

The sex ratio of 215 reindeer foetuses from six wild reindeer herds in southern Norway did not differ from parity among ranges, among sampling years or in the total sample. Results are consistent with theory and recordings on *Rangifer* foetuses (Thomas, Barry & Kiliaan 1989, Kojola & Helle 1994, Reimers & Lenvik 1997) and on newborns (Kojola & Eloranta 1989). Skogland (1986), whose data are partly included in the present analyses, arrives at another conclusion implying a rather elaborate but unsubstantiated hypothesis frequently referred to in the literature:

1) Among small-sized, resource limited females with high mortality of progeny during parental investment, the prenatal sex ratio favoured males. After weaning, at the end of juvenile male dispersal, the ratio has been skewed in favour of females.
2) Among large-sized, well fed females without postnatal offspring mortality, the pre- and post-weaning sex ratio favoured females. A recalculation of Skogland's (1986) skewed prenatal sex ratios ($\chi^2 = 11.06$; $P < 0.01$) gives a non-significant $\chi^2 = 2.73$.

Even though the overall foetus sex ratio did not vary from parity this does not exclude a non-parity age and weight relationship as hypothesised by Trivers & Willard (1973). No such relationship was found among wild reindeer (see Tables 2 and 3), among domestic reindeer (Kojola & Helle 1994, Reimers & Lenvik 1997) or Peary caribou *Rangifer t. pearyi* (Thomas et al. 1989). Kojola & Eloranta (1989) found that the newborn sex ratio related to maternal body weight in semi-domestic reindeer, and Thomas et al. (1989) reported a maternal age effect in barren ground caribou *Rangifer t. groenlandicus* from the Beverly herd. Both maintain support for the Trivers & Willard (1973) hypothesis predicting that females in better condition bear more male progeny. Their data support is commented upon elsewhere (Reimers & Lenvik 1997).

Manipulation of sex ratios at conception or differential mortality *in utero* are two ways the female may regulate the sex of her offspring. In the absence of any known mechanism by which sex ratios at conception can be manipulated (e.g. Williams 1979), differential mortality *in utero* is a possible mechanism. Reindeer males are born heavier than females (Varo 1972). However, foetus sex weight differences were small (≤204 g) and insignificant during February and March. Thomas et al. (1989) also found no significant weight difference between male and female foetuses from Peary and barren ground caribou. They, however, reported that female barren ground caribou in the >10 year class bore significantly more and heavier (214 g) male than female foetuses. They indicated that this male-dominated sex ratio could be of selective advantage: "Old females would pass on more genes to future generations if they produced males that became top ranked when they matured or males that achieved high social rank at an earlier age than others. The males produced by old females are likely to be more successful as breeders than males produced by young females because they may learn how to dominate others by mimicking the domineering behaviour of their mothers, and they may have a higher birth weight and grow faster than males produced by young mothers". This speculation appears possible, but remains unsubstantiated.

It appears unlikely that the foetus weight differences observed could cause maternal nutritional stress resulting in differential *in utero* mortality. Abortions occurring in reindeer under severe nutritional stress (Tyler 1987), can cause a higher loss of male than of female foetuses as indicated by Kojola & Helle (1994). Pregnancy rates measured in early as well as in late winter in adult domestic and wild reindeer varies from close to 100% in females in good condition to around 80% in females in poor condition (Reimers 1997). These rates apparently remain stable until April, and hence, do not leave much room for differential *in utero* mortality as is also indicated by the lack of foetus sex differences in *Rangifer*.

Trivers & Willard (1973) based their hypothesis on three assumptions:

1) The condition of the young tend to be correlated with the condition of the mother during parental investment.
2) Differences in the condition of young at the end of the period of parental investment tend to endure into adulthood.
3) Adult males will be differentially helped in reproductive success (compared to adult females) by slight advantages in condition.

As discussed in Reimers & Lenvik (1997) the first of these assumptions is supported (Reimers, Klein & Sørumgård 1983, Lenvik & Fjellheim 1988). The second assumption is questionable. A female body mass of 40 kg at six months of age explains 50% of the body mass at 18 months of age (Lenvik & Fjellheim 1988). If she weighs 50 kg or more, the prediction power falls to 10% because heavy calves are likely to breed, and early pregnancy affects their growth, their future reproduction (Reimers 1983) and the survival of their first calves (Lenvik & Aune 1988). In a sample of 74 calves with similar weights at six months (50 kg), 13 got pregnant and weighed the same at the age of 16 months, compared to an average weight of 63.4 kg among their barren sisters (Lenvik & Fjellheim 1988). Calf mortality during the first two months dropped from 48% among mothers weighing 55 kg to 2-4% among mothers weighing 70 kg or more (Lenvik & Aune 1988).

The third assumption states that in theory, slight advantages in condition should have disproportionate effects on male reproductive success compared to the effect on female reproductive success because males compete to inseminate females. However, breeding success in males is primarily related to age, antler size and body size (Espmark 1964, Kojola 1991, Hirotani 1994). Due to compensatory growth, any individual and temporary growth setback during early life will be small and probably insignificant as will the effect on the socially important antlers. Although sexually mature at an age of six months, these young male reindeer are prevented from breeding until older age by the older males. In reindeer, breeding mostly takes place during two weeks in October in herds frequently counting several hundred animals with individual adult males guarding individual females. The high number of adult three year or older males in the wild reindeer herds (35-50 males per 100 females aged one year or older; E. Reimers, unpubl. data) possibly prevents any male from maintaining any measurable advantage in breeding success beyond that which age and experience allow. In domestic reindeer herds where the number of males are kept at a minimum, it is conceivable that individual males will benefit due to lack of competition. However, the breeding male component in the sampled herds ranged from 20 to 33 males per 100 females (Lenvik, Granefjell & Tamnes 1988) without causing a non-parity foetus sex distribution.

No data on individual male reproductive success relating to body weight or antler size are available. Neither in this study nor in that of Reimers & Lenvik (1997) did heavy-weight reindeer females carry more male foetuses. This may indicate that the third assumption of Trivers & Willard (1973) fails to be acknowledged by reindeer.

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