

Offspring sex ratio adjustment in reindeer, *Rangifer tarandus*

Ilpo Kojola & Timo Helle

Kojola, I., Finnish Game and Fisheries Research Institute, Reindeer Research, FIN-99910 Kaamanen, Finland

Helle, T., The Finnish Forest Research Institute, Rovaniemi Research Station, P.O. Box 16, FIN-96301 Rovaniemi, Finland

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Theoretically parents should be able improve their fitness by adjusting the offspring sex ratio. Trivers & Willard (1973) predicted that in polygynous mammals mothers in superior condition should produce more males than weaker females. *Rangifer tarandus* (reindeer and caribou) is one of the most polygynous large mammals. However, we did not find any differences in body size, fat reserves or age between semi-domesticated reindeer (*R. t. tarandus*) females carrying male or female fetuses. Our results challenge Trivers & Willard's model, and one hypothetical reason for the lack of firm supportive evidence is the variability in winter foraging conditions that may weaken the link between parental investment and offspring sex ratio.

1. Introduction

Much attention has been paid to the possible adaptiveness of the variation in offspring sex ratios in mammals. One of the main questions has been whether the observed sex ratios are subject to modification based on maternal condition. Many predictions have been based on the hypothesis that parental investment may have different effects on reproductive success of sons and daughters (Trivers & Willard 1973, Maynard Smith 1980, Clutton-Brock & Albon 1982). In a polygynous breeding system, where males' fighting ability largely determines their access to receptive females, male fitness evidently depends

more strongly on early growth rates and hence mothers' ability to invest in reproduction (Clutton-Brock et al. 1984, Meikle et al. 1984). Accordingly, heavier maternal investment in sons than daughters may be expected. One way in which this can be done is that mothers in better condition produce more sons (Trivers & Willard 1973, Clutton-Brock et al. 1981, 1984). This could be potentially come true by increased mortality of male embryos under nutritional stress (Clutton-Brock & Iason 1986, Clutton-Brock 1991). Parents can accomplish preferential investment also by investing relatively more in sons than daughters: for example, male offspring birth weights can be higher and they may suckle more than

female offspring (Reiter et al., 1978, Clutton-Brock et al. 1981, Maynard Smith 1980, Trillmich 1986, Verme 1989, Kojola 1993).

Rangifer tarandus (reindeer and caribou) is one of the most polygynous large mammals (Clutton-Brock et al. 1980, Jarman 1983, Skogland 1989). Trivers & Willard (1973) used this species as an empirical example in their maternal condition hypothesis in which they suggested that superior females should produce more males than weaker females. In this paper we investigate whether female body size, fat reserves and age affect fetal sex in semi-domesticated reindeer, and discuss the available evidence of progeny sex ratio variation in this species in the light of Trivers & Willard's hypothesis.

2. Material and methods

We collected 484 reindeer fetuses from three semi-domesticated reindeer (*R.t. tarandus*) herds in January 1991 (Ivalo) and 1992 (Muotkatunturi and Näkkälä) in northern Finland. Fetuses were sexed and weighed. The most commonly used and widely accepted indicators of physiological condition are body weight and fat reserves (Riney 1982). Reindeer females were measured for back length, dressed weight (live weight minus head, skin, viscera, blood and metabodials) and back fat depth. Back fat is closely correlated with Kidney fat index in female reindeer (Tyler 1987). Most females ($N = 411$) were aged by cementum analysis from incisors at Matson's Laboratory, Montana. To assess whether females carrying male vs. female fetuses were in different condition we carried out two-way multiple ANOVAs in which herd and fetal sex were treated as independent and back fat depth, age and size indices (dressed weight in one model, back length in another) were treated as dependent variables. Because age was not known for all females, models both with and without age were performed. Sex ratios were compared by use of G-test or Fisher's exact test.

3. Results and discussion

The proportion of males was 62.2% ($N = 180$) in Ivalo, 53.3% ($N = 92$) in Muotkatunturi and 57.1%

($N = 212$) in Näkkälä. Sex ratios did not differ between herds ($G = 2.23$, $df = 2$, $P = 0.328$). A slight, non-significant male bias was found in all female age classes (Table 1). Results from multiple ANOVAs in which weight and back fat were treated as dependent variables showed herd differences in female characteristics (Wilks' $F = 69.781$, $df = 4, 878$, $P < 0.001$), but the sex of the fetus was not connected with the variation of these variables ($F = 0.181$, $df = 2, 439$, $P = 0.834$). The entering of female age as a third dependent variable yielded almost similar results (the effect of herd: $F = 41.497$, $df = 6, 764$, $P < 0.001$; the effect of sex: $F = 0.313$, $df = 3, 382$, $P = 0.816$). Females in Ivalo were larger and younger, and they had more back fat than females in Muotkatunturi or Näkkälä, but any of the female characteristics did not vary by the sex of the fetus (Table 2 and Table 3).

The weight of male fetuses (mean \pm SE 245 \pm 12 g) depended on mother's weight in Ivalo ($r = 0.316$, $P = 0.001$) and Muotkatunturi ($r = 0.594$, $P < 0.001$) but not in Näkkälä ($r = 0.174$, $P = 0.058$). The weight of female fetuses (207 \pm 12 g) did not depend on mother's weight in any herd (P values > 0.10). Male fetuses were heavier than female fetuses (Student's $t = 2.42$, $P = 0.016$). Neither the weight of male nor female fetus was correlated with female back fat depth (P values > 0.05).

Our results did not support Trivers & Willard's (1973) hypothesis of parental ability to improve fitness by adjusting the offspring sex ratio, thereby deviating from many indications of such an ability in mammals (Clutton-Brock et

Table 1. Fetal sex ratio variation in relation maternal age in three semi-domesticated reindeer herds, northern Finland.

Mother's age	% males	N
2	53.1	49
3	60.7	51
4	57.4	54
5	54.2	48
6	72.7	44
7-8	51.4	74
9-10	55.9	34
>10	59.7	57

al. 1981, Simpson & Simpson 1982, Silk 1983, Meikle et al. 1984, Austad & Sunquist 1986, Rutberg 1986, Kojola & Eloranta 1989). Results from previous investigations on fetal sex ratios in mammals are not firmly consistent with Trivers & Willard (1973) hypothesis. Improved feeding conditions in the opossum, *Didelphis marsupialis* (Austad & Sunquist 1986), and female barrenness in bison, *Bison bison* (Rutberg 1986), increased the proportion of males, but no association was found between mother's fat reserves and the gender of the fetus in rhesus macaques, *Macaca radiata* (Berman 1988) or in arctic caribous, *Rangifer tarandus groenlandicus* and *R.t. pearyi* (Thomas et al. 1989).

Evidence of sex ratio adjustment in *Rangifer tarandus* is rather inconclusive: three of five studies appear to contain results that support Trivers & Willard's (1973) hypothesis, but none of these presents strong supportive evidence (Table 4 and 5). In Norwegian wild reindeer, the largest proportion of males appears to be born in food-limited conditions (Skogland 1986). Skogland's (1986) interpretation for this finding is based on Fisher's (1930) sex ratio equilibrium theory: owing to male-biased newborn mortality,

fitness costs of producing male sex are cheaper and therefore males are produced most in poorest range. We suggest that his results do not necessarily contradict Trivers & Willard's (1973) maternal condition hypothesis (but see Caley & Nudds 1987): females whose newborn have died may be in superior condition at conception because they have been freed from the costs of lactation. Summer body weight gain of such females are essentially greater than that of lactating females (Eloranta & Nieminen 1991). Moreover, Kojola & Eloranta (1989) showed that females whose calves had died during the first month following birth produced a significant excess of males in the subsequent year. Only 45% of calves survived upto weaning in the poorest Norwegian range, and male calf mortality was about 40% higher than female calf mortality, while in good range no preweaning mortality existed (Skogland 1986). We conclude that Skogland's (1986) results are indifferent in the light of Trivers & Willard's model. Thus they appear to belong to the same category as results obtained in this study (Tables 4 and 5).

The key factor in studies of sex ratio variation in *Rangifer tarandus* varies from study to

Table 2. Dressed weight, back length, back fat depth and age of female reindeer (means±SE) carrying male and female fetuses in three semi-domesticated herds, northern Finland.

Herd	Sex of fetus	Weight (kg)	Back fat (mm)	Length (cm)	N	Age (yrs)	N
Ivalo	female	32.84±0.55	16.46±1.13	75.16±0.48	74	3.04±0.44	47
	male	33.53±0.53	16.80±0.75	75.11±0.39	106	4.04±0.32	85
Muotkatunturi	female	28.46±0.68	4.64±1.10	72.74±0.57	43	5.71±0.47	41
	male	28.05±0.52	5.27±1.06	72.98±0.53	49	5.57±0.45	44
Näkkälä	female	28.21±0.36	4.00±0.61	73.44±0.35	91	5.63±0.33	82
	male	28.15±0.35	3.80±0.57	73.67±0.29	121	5.32±0.28	112

Table 3. The effects of herd and fetal sex on reindeer female weight, back fat depth back length and age in three semi-domesticated herds, northern Finland.

Dependent variable	Independent variables				Two-way interaction	
	Herd		Sex		Herd × sex	
	F	P	F	P	F	P
Weight	67.26	<0.001	0.15	0.701	0.49	0.616
Back fat	155.45	<0.001	0.14	0.712	0.13	0.876
Length	13.75	<0.001	0.15	0.697	0.07	0.928
Age	18.52	<0.001	0.34	0.561	1.90	0.151

study (Tables 4 and 5). Data sets are so few that it is premature to estimate how this variability is attributed for example to different environmental

conditions. One reason may be the fact that some analyses are based on relatively small sample sizes. As mentioned above, maternal fat reserves

Table 4. Birth sex ratio adjustment in *Rangifer tarandus* in relation to Trivers & Willard (1973) hypothesis (see text for more details).

<i>R.t.tarandus</i>		Main results			Supportion to T&W hypothesis
Semi-domesticated	Female age (years)	% males	<i>N</i>		
		3	0.0	9	
		4	52.2	46	
		5	47.6	21	yes(?) ¹⁾
Wild	Range quality	% males	<i>N</i>		
		poor	53.5	101	
		medium	47.6	176	
		good	40.1	40	no ²⁾
Semi-domesticated	Mother's weight (kg)	% males	<i>N</i>		
		<61	38.5	83	
		61–70	50.4	349	
		71–80	54.7	351	
		>80	52.0	100	
	Mother's age	no effect			yes ³⁾

Source: ¹⁾ Varo 1964, ²⁾ Skogland 1986, ³⁾ Kojola & Eloranta 1989, 1990

Table 5. Fetal sex ratio adjustment in *Rangifer tarandus* in relation to Trivers & Willard (1973) hypothesis (see text for more details).

Subspecies	Main results			Supportion to T&W hypothesis
<i>R.t.tarandus</i> , semi-domesticated	Mother's age no effect	Body size no effect	Fat reserves no effect	no ¹⁾
<i>R.t.groenlandicus</i> , wild	Mother's age (years)	% males	<i>N</i>	
		2–4	37.8	127
		5–7	51.7	149
		8–10	50.5	99
	>10	67.4	46	
	Mother's fat reserves no effect	Body size no effect		yes(?) ²⁾
<i>R. t. pearyi</i> , wild	Mother's age (years)	% males	<i>N</i>	
		2–4	39.1	23
		5–7	45.8	24
		8–10	52.4	21
	Mother's body size no effect	Fat reserves no effect		no ²⁾

Source: ¹⁾ This, study, ²⁾ Thomas et al. 1989

did not differ by the gender of the fetus in arctic caribous, but youngest females were found to produce more daughters (Table 5; Thomas et al. 1989). We have found similar evidence from Varo's (1964) investigations on semi-domesticated reindeer (Table 4). In his data the youngest, three-year-old females produced nine female but no male calves, while four-year-old and five-year-old females gave birth to 33 female and 34 male calves. These sex ratios are significantly different (Fisher's exact $P = 0.003$). However, twelve-year data comprising 883 births within an experimental herd in northern Finland maternal age did not influence offspring sex ratio (Kojola & Eloranta 1989). In this herd the only influential characteristic was female body weight owing to the excess of female calves born to the females weighing less than 60 kg, at which they have a sharp increase in fertility (Table 4; Kojola & Eloranta 1989).

The relationship of female age to her capacity to invest in reproduction may be complex. Social dominance status that affects access to limited winter foods is often lowest among the youngest reproductive females, but age usually has smaller effect than body weight (Kojola 1989). Largest samples in our fetal sex ratio data were collected from herds occupying badly depleted winter ranges (Kojola et al. 1993), where rapid tooth wear can decrease the advantage of higher social status associated with ageing (see Skogland 1988).

Two general features can be figured out from available evidence concerning sex ratio adjustment in *R. tarandus*. First, results are not invariably supportive to Trivers & Willard (1973) hypothesis. Second, whenever some measure of mother's ability to invest in offspring has been detected to be correlated with sex ratio, it appears that usually the most food-limited females produce sex ratios that deviate from unity: they avoid to produce male sex. This finding suggests that different sexes have different thresholds of female condition. Because such a feature has not been found in any temperate or tropical mammal (Clutton-Brock & Iason 1986), it may have something to do with the hardship of winter-time gestation period. One potential way by which this could come true is the exacerbation of male

fetus mortality under nutritional stress (Clutton-Brock 1991). So far this has been documented for a laboratory stock of golden hamster (*Mesocricetus auratus*) only (Labov et al. 1986). There exists evidence that abortions are common in Svalbard reindeer (*R. t. platyrhincus*) under nutritional stress (Tyler 1987), and our results from semi-domesticated reindeer show that when food limitation is severe enough to entail a major loss of reproductive rate during late winter, more female than male calves are born in the spring (Kojola & Helle, unpublished data). Because size of male fetuses appeared to be more correlated with mother's size, one potential reason for the higher mortality of male fetuses may be simply their higher nutritional demands. Even if this were not the case, the abortion of male fetus saves the weak female from costs of producing small, weak males that have only marginal chances to reproduce in polygynous breeding system. Differential fetal mortality might be based also on mother's ability to recognize sex differences in the hormonal activity of the fetus (Glucksmann 1974).

Development of condition-size relationship in differential snow conditions could be of crucial interest also, because it offers a hypothetical explanation why reindeer and caribou data are rather weakly supportive to Trivers & Willard's (1973) model. The thickness and hardness of snow affect energy expenditure of moving and foraging in reindeer (Fancy & White 1985). Because the amount of maintenance energy is correlated with body size and snow conditions vary annually, male breeding success is not necessarily much enhanced by exceptionally heavy maternal investment. Moreover, it could be useful to have some estimates of the influence of maternal investment on daughter's reproductive success. Kojola (1989) has shown that mother's dominance status affects more female than male calf's weight loss during winter, because female calf shares feeding crater with her mother more often than male calf, but the effects on daughter's breeding are not known.

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References

- Austad, S. N. & Sunquist, M. E. 1986: Sex-ratio manipulation in the common opossum. — *Nature* 324: 58–50.
- Berman, C. M. 1988: Maternal condition and offspring sex ratio in a group of free-ranging rhesus monkeys: an eleven-year study. — *Amer. Nat.* 131: 307–328.
- Clutton-Brock, T. H. 1991: *Evolution of parental care*. Princeton Univ. Press, Princeton.
- Clutton-Brock, T. H. & Albon, S. D. 1982: Parental investment in male and female offspring in polygynous mammals. — In: King's College Sociobiology Group (ed.), *Current problems in sociobiology*: 223–247. Cambridge Univ. Press, Cambridge.
- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1981: Parental investment in male and female offspring in mammals. — *Nature* 289: 487–489.
- 1984: Maternal dominance, breeding success and birth sex ratio in red deer. — *Nature* 308: 358–360.
- Clutton-Brock, T. H. & Iason, R. V. 1986: Sex ratio variation in mammals. — *Quart. Rev. Biol.* 61: 339–374.
- Eloranta, E. & Nieminen, M. 1991: Lactational control of fertility and calf production in Finnish reindeer. — In: Bobek, K., Perzanowski, K. and Regelin, W. L. (eds.), *Global trends in wildlife management: Transactions of the 18th Congress of the International Union of Game Biologists*, Jagellonian University, Krakow, Poland, 22–29 August 1987: 197–200. Swiat Press, Krakow and Warsaw.
- Fancy, S. G. & White, R. G. 1985: Energy expenditures of caribou while cratering in snow. — *J. Wildl. Manage.* 49: 987–993.
- Glucksmann, A. 1974: Sexual dimorphism in mammals. — *Biol. Rev.* 49: 433–474.
- Helle, T., Aspi, J. & Pullianen, E. 1987: Size-related changes in winter condition of male calves in reindeer. — *Rangifer* 7(1): 2–11.
- Jarman, P. 1983: Mating systems and sexual size dimorphism in large, terrestrial mammals. — *Quart. Rev. Biol.* 58: 485–500.
- Kojola, I. 1989: Mother's dominance status and differential investment in reindeer calves. — *Anim. Behav.* 38: 177–185.
- 1993: Early maternal investment and growth in reindeer. — *Can. J. Zool.* 71: 753–758.
- Kojola, I., Aikio, P. & Helle, T. 1993: Luontaisten ravintovarojen vaikutus porotalouteen Pohjois-Lapissa. — Univ. Oulu, Res. Inst. Northern Finland, Res. Rep. 116. 39 pp.
- Kojola, I. & Eloranta, E. 1989: Influences of mother's body weight, age and parity on sex ratio in semi-domesticated reindeer (*Rangifer t. tarandus*). — *Evolution* 43: 1331–1336.
- 1990: Reproductive investment by females in semi-domesticated reindeer. — *Rangifer*, Special Issue 3: 343–349.
- Labov, J. B., Huck, U. W., Vaswani, P. & Lisk, R. D. 1986: Sex ratio manipulation and decreased growth of male offspring of undernourished golden hamsters. — *Behav. Ecol. Sociobiol.* 18: 241–249.
- Maynard Smith, J. 1980: A new theory of sexual investment. — *Behav. Ecol. Sociobiol.* 7: 247–251.
- Meikle, D. B., Tilford, B. L. & Vessey, S. H. 1984: Dominance rank, secondary sex ratio and reproduction of offspring in polygynous primates. — *Amer. Nat.* 124: 173–188.
- Preobrazhenskii, B. V. 1961: Management and breeding of reindeer. — In: Zhigunov, P. S. (ed.), *Reindeer husbandry*: 78–128. Israel Prog. Sci. Transl. Jerusalem.
- Reiter, J., Stinson, N. L. & LeBoeuf 1978: Northern elephant seal development: the transition from weaning to nutritional independence. — *Behav. Ecol. Sociobiol.* 3: 337–367.
- Rutberg, A. T. 1986: Lactation and fetal sex ratios in American bison. — *Amer. Nat.* 127: 89–94.
- Skogland, T. 1986: Sex ratio variation in relation to maternal condition and parental investment in wild reindeer. — *Oikos* 46: 417–419.
- 1989: Comparative social organization of wild reindeer in relation to food, mates and predator avoidance. — *Adv. Ethol.* 29: 1–71.
- Thomas, D. C., Barry, S. J. & Kiliaab, H. P. 1989: Fetal sex ratios in caribou: maternal age and condition effects. — *J. Wildl. Manage.* 53: 885–890.
- Trillmich, F. 1986: Maternal investment and sex-allocation in the Galapagos fur seal, *Arctocephalus galapagoensis*. — *Beh. Ecol. Sociobiol.* 19: 157–164.
- Trivers, R. L. & Willard, D. E. 1973: Natural selection of parental ability to vary the sex ratio of offspring. — *Science* 179: 90–92.
- Tyler, N. J. C. 1987: Natural limitation of the abundance of high arctic Svalbard reindeer. — Phd. thesis. University of Cambridge.
- Varo, R. M. 1964: Tutkimuksia poron jalostusmahdollisuuksista. — *Ann. Agric. Fenn.* 3: 296–310.
- Verme, L. J. 1989: Maternal investment in white-tailed deer. — *J. Mammal.* 70: 438–442.