Reproductive investment by females in semi-domesticated reindeer

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Abstract: This paper discusses maternal investment in a herd of semi-domesticated reindeer in Kaamanen, Finnish Lapland (69°N 27°E). Male-producing cows weighed 2% more at the previous conception then the female-producing cows did. The body weight of cow accounted for more of the variation of birth sex ratio than the age or the parity. The lightest cows (<61 kg) produced a significant excess (62%) of female calves. Both the medium-sized and the largest cows gave birth to a slight, nonsignificant excess of males. In terms of weight change from one conception to the next, rearing a male to weaning was more expensive to cows than rearing a female. The frequency of reproductive failures did not, however, depend significantly upon the sex of the previous calf. The survival and growth of male and female calves related in an approximately similar fashion to maternal weight.

Key words: Sex ratio, maternal investment

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Introduction

Theoretical treatment of parental investment has evoked a hypothesis which predicts that parents should invest more heavily in the sex among which reproductive success varies more widely (Trivers, 1972; Maynard Smith, 1980; Meikle *et al.*, 1984). this sex is commonly suggested to be the male. Trivers and Willard (1973) have predicted that parents can improve their fitness by controlling the sex ratio of their offspring. They have hypothesized that in polygynous breeding system mothers in good condition should produce more male offspring whilst those in poorer condition should produce more female offspring. Parents can accomplish preferential investment also by investing relatively more in individual males than in individual females (Reiter *et al.,* 1978; Trillmich, 1986), or vice versa (Hoogland, 1981; Caley and Nudds, 1987). In several polygynous mammals, maternal investment before weaning is greater for males than for females (Reiter *et al.*, 1978; Clutton-Brock *et al.*, 1981; Kovacs and Lavigne, 1986; Lee and Moss, 1986; Trillmich, 1986). In polygyny males are more likely than females to disperse as juveniles (Greenwood, 1980; Dobson, 1982). Post-weaning resource competition between mother and female offspring in natal groups may conterbalance heavier investment given in males (Clutton-Brock *et al.*, 1981) or even make females the more expensive sex (Hoogland, 1981; Caley and Nudds, 1987).

Reindeer exhibits a very pronounced sexual dimorphism in size. In wild herds, adult bulls weigh twice as much as adult cows (Skogland, 989). This indicates an intense male-male competition for mates and, accordingly, a high degree of polygyny (see Trivers, 1972; Clutton-Brock et al., 1980). The variance of lifetime breeding success should therefore be diffeential for males and females. We may expect that dominant, large-bodied females produce more male offspring than subordinate, more ood-limited females do. Provided that female eindeer invest more heavily in male than in female offspring, the sex of the offspring raised hould influence the weight change of mother between two consecutive autumns. The barrenness in the subsequent year could also be more common after weaning a male than weaning a female calf (Clutton-Brock *et al.*, 1981; Wolff, 988).

This short review draws together the most essential issues of papers dealing with sex ratio and maternal investment within the herd of semi-domesticated reindeer in Kaamanen, Finnish Lapland (Kojola, 1989a; 1989b; Kojola and Eloranta, 1989). Herein we also consider data on sex ratio and available information of maternal investment revealed in other studies of reindeer and caribou.

Material and methods

The data were collected in 1970-1987. The number of reproductive females varied annually between 29-93. Reindeer were permitted to move freely within an enclosed pasture of 70 km^2. From December to June, reindeer were supplementarily fed. During other seasons they met their energy demands by grazing natural vegetation. Reindeer were weighed in autumn, usually in November. Before the calving period (May) reindeer were gathered to give birth to their calves in a 10 hectare enclosure. During calving, newborns were daily sought out, sexed and weighed. Most calves (50% of females, 85% of males) were slaughtered in autumn. Data comprise of 1087 reproductions. Maternal body weight was known in 849 cases. In 1985-1986, reindeer were weighed also in the end of April and in the middle of June.

Results

In 1970-1987, sex ratio was 51.2% males at birth and 50.5% males one month after weaning. The cows which produce male calves weighed 2% more in November the preceding autumn than the cows which gave birth tc female calves (means of 71.7 and 70.4 kg, respectively). This difference was statistically significant (t=2.46, p=0.012, df=849; Kojola and Eloranta, 1989). Weights for females females ageing 2-4 years did not differ with the sex of the subsequent offspring (Fig. 1). As regards parity, weights were different for females carrying their fourth or fifth offspring (Fig. 1).

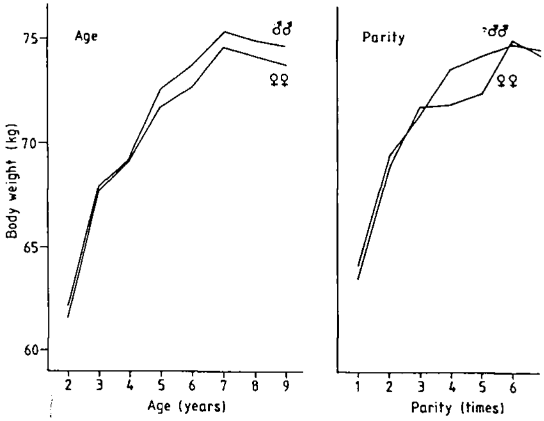

Fig. 1. Post-breeding weights of cows as functions of maternal age (left) and parity (right) are shown separately according to sex of the subsequent progeny. (Kojola and Eloranta, 1989). Statistical tests are given in the text.

The sex of the calf accounted for more of the variation in the maternal body weight than maternal age (F=5.4, df=1.880, p=0.020) or the parity (F=4.4, df=1.713, p=0.036) (hierarchi-

Table 1. Progeny sex ratio for mothers of different weight categories. P values are from binomial tests.

Maternal body weight (kg)	Males (%)	n	p
< 61	38.5	83	0.048
61-65	45.9	135	0.655
66-70	53.5	214	0.648
71-75	53.1	213	0.696
76-80	57.2	138	0.229
> 80	52.0	100	0.764
Totals	51.2	883	0.812

cal analyses of variance in which weight, age and parity were treated as independent variables; Kojola and Eloranta, 1989). Cows weighing equal or less than 60 kg (at which there was a sharp increase in fertility; see Eloranta and Nieminen, 1986) produced a significant excess of females (Table 1). Both the medium-sized and the largest females produced a slight, nonsignificant excess of male calves (Table 1). An analysis of sex-ratio variation for mothers within different combinations of parity showed that three-year old first-breeders (mean weight 66.7 kg) produced significantly more males than the two-year old first-breeders (mean weight 61.9 kg) did 62.7%, n=69 and 45.1%, n=122, respectively, chi-square test, $p=0.041$). Among other categories of parity, sex ratio (or the maternal weights) did not differ with the age (Kojola and Eloranta, 1989).

Measured as a weight change from one conception to the next, rearing male to weaning resulted in greater energetic demands on cow than rearing a female (difference in proportional weight change was 2%; an analysis of variance; cow weight and age were treates as covariated; $F=5.7$, df=3,527 $p=0.018$; Kojola and Eloranta, 1989). The sex ratio which preceded barrenness did not, however, deviate significantly from 1:1 (56.1% males; n=82, chi-square test; $p > 0.10$). Female offspring up to the age of 4 years tended to remain close to their mother (Kojola and Nieminen, 1988; Kojola 1989c). The number of female offspring present (range 0-3) did not affect maternal weight change between consecutive years (Kojola, 1989b). During the first post-weaning winter female calves share snow craters with their mother twich as often as did male calves (Kojola, 1989a). The weight change of mother did not however depend on the sex of the calf (Kojola, 1989a).

The mortality rate of male and female calves before weaning depended in appoximately similar fashion on maternal body weight (sex ratio of died calves did not deviate from 1:1 or from the sex ratio produced within different categories of body weight (class spaces of 5 kg) or age; chi- square tests, p values > 0.10). Maternal body weight accounted for 21% of variation in autumn weights both for male and female calves (linear regression models; p values <0.001).

Discussion

There is much recent evidence for mammals giving support to the Trivers and Willard's (1973) "maternal condition hypothesis" which predicts that superior females produce more females than weak females do (Clutton-Brock *et al.*, 1981; Burley, 1982; Meikle *et al.*, 1984; Austad and Sunquist, 1986, 1986; Huck *et al.*, 1986, Rutberg, 1986; Wright *et al.*, 1988). In many mammalian populations, however, results are contradicting: well-fed females overproduce daughters (Simpson and Simpson, 1982; Silk, 1983; Verme, 1983; Skogland, 1986; Silk, 1988). In mammals, males usually equal or outnumber females at birth (Parkes, 1926; Clutton-Brock and Iason, 1986). This seems to be the case in *Rangifer tarandus*, too (Kelsall, 1968; Espmark, 1971; Nowosad, 1975; Kojola and Eloranta, 1989). Results revealed for reindeer and caribou are not invariably supportive to the model of Trivers and Willard (1973). In a study by Varo (1964) of semi-domesticated reindeer, first-breeding, small females produce more female calves than the older ones. In the herd studied by us, the sex ratio of calves born to the first-breeders did not deviate from unity or from the sex ratio of calves born to older females (Kojola and Eloranta, 1989). In caribou (*R.t. pearyi* and *R. t. groenlandicus),* young females carry more often female fetuses than the older ones (Thomas, 1988). In ungulates, female social rank usually increases with the age (Rutberg, 1981; Townsend and Bailey, 1981; Hall, 1983). In wild reindeer, however, more female are born in rich than in poor habitat (Skogland, 1986). It is fair to notice, as has been pointed out by Clutton-Brock and Iason (1986), that sex-ratio trends are not likely to be explained by one adaptive theory. Results revealed for wild reindeer coincide well with Fisher's (1930) argument that parents should overproduce the more cheaper sex: on poor range, highter mortality rate of male calves tends to decrease costs associated with producing males (Skogland, 1986). On a variety of primate populations, sex-ratio trends are likely to be explained by the resource competition model, which implies that overt female-female competition for access to locally limited resources in natal groups makes maternal social rank more important for survival and breeding success of female offspring than for those of male offspring (Silk, 1983; 1988; see also McFarland Symington 1987 for a species in which males are the more sedentary sex). Well-fed white-tailed deer *(Odocoileus virginianus)* females produce more female fawns than do females that are nutritionally deprived (Verme, 1969). On the other hand, the proportion of male fawns decreases with the increasing litter size (Verme, 1983). Since the litter size is likely to affect the intensity of reproductive effort white-tailed does are likely to produce one male fawn whenever not able to successfully rear two fawns (see Williams, 1979). Caley and Nudds (1987) have challenged this idea and suggested that the increased female-female competition for food in poor habitat makes the females the more expensive sex and hence brings about a male-bias for offspring (see Fisher, 1930 for theoretical background).

Body weight of cow is a measure which is closely correlated with social rank (Kojola, 1989a). Access to food is favored by high social rank. Therefore we may expect large-bodied females to have higher-than-average capacity to invest in reproduction. In this paper we consider maternal post-breeding weights as an indicator of mother's quality. This measure is likely to predict maternal ability to allocate resources to progeny during gestation as well as postnatally. In two unprovisioned winter herds in Kaamanen, large-bodied, high-ranking females were able to maintain their body weight proportionately better than lower-ranking females (Kojola, 1989a).

Our results are not unambigiously supportive to the Trivers and Willard's (1973) "maternal condition hypothesis". The very smallest cows overproduced females, as is initially predicted by the model, but the sex ratio produced by the very largest cows did not deviate from unity or from the sex ratio of offspring born to the middle-sized cows.

Measured as the weight change of mother, rearing a male offspring to weaning was more costly than rearing a female offspring. This did not occur at a cost to mother's reproductive success in the subsequent year, however. This result deviates form that revealed for red deer on Rhum, Scotland, where hinds more often fail to reproduce after a male than after a female calf (Clutton-Brock et al., 1981; see also Wolff (1988) for bison *(Bison bison)* in Montana).

Reindeer give birth to their calves soon after a period of increased resource competition and before the burst of vegetation. Therefore females which show the lowest competitive ability might reach best reproductive success by investing predominantly in the sex that needs less maternal resources for survival or being reproductive in adulthood. Helle et al. (1987) have shown that on poor winter ranges the very largest as well as the very smallest male calves lose their fat depots sooner than do the medium-sized calves. Such normalizing selection may weaken the association between maternal investment and male reproductive success is not necessarily much enhanced by exceptionally heavy maternal investment (Kojola, 1989b). In the reindeer herding district of Finland, winter ranges have been poor during this entire century (Helle, 1982). This provides one potential explanation for the marginality of the difference in maternal investment given for male vs. female offspring.

Females invested more heavily in male than female offspring during gestation and during the first life weeks of the calf. Male calves weigh 6% more than female calves at birth (Eloranta and Nieminen, 1986). When giving birth to a male, cows lose more body weight than when giving birth to a female (10.3 ± 0.8% (SE) with a female, 12.8 ± 0.6% with a male offspring; expressed as proportional weight change from the end of April to the middle of June; $F=4.2$, $df=1, 112$, $P<0.05$; data for 1985-1986; Kojola 1989b). Male calves are permitted to suckle more than female calves during the first month postnatally (Kojola, 1989b). From June to November, cows investing in males were able to recover from the heavier weight loss they suffered during calving (Kojola, unpublished). Herbivores of tundra and northern taiga have to meet the demands of short growth period and strict seasonality of resources. These selection pressures result in birth synchrony (Berglund, 1975; Skogland 1989). There is evidence that body condition influences the timing of conception (Skogland 1989). Therefore cows that produce male calves should be able to recover from their heavier investment before next breeding season.

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