BIOLOGICAL RESEARCH REPORTS FROM THE UNIVERSITY OF JYVÄSKYLÄ

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UNIVERSITY OF JYVÄSKYLÄ, JYVÄSKYLÄ 1989

BIOLOGICAL RESEARCH REPORTS FROM THE UNIVERSITY OF JYVÄSKYLÄ

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URN:ISBN:978-951-39-8828-9
ISBN 978-951-39-8828-9 (PDF)
ISSN 0356-1062

Jyväskylän yliopisto, 2022

ISBN 951-680-092-0
ISSN 0356-1062

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Jakaja *Jyväskylän yliopiston kirjasto 40100 Jyväskylä*
Distributor *Jyväskylä University Library SF-40100 Jyväskylä Finland*

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FROM THE
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Academic Dissertation

To be presented, with the permission of the Faculty of Mathematics and Natural Sciences of the University of Jyväskylä, for public criticism in Auditorium S 212, on May 20, 1989, at 12 o'clock noon.

UNIVERSITY OF JYVÄSKYLÄ, JYVÄSKYLÄ 1989

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Biol. Res. Rep. Univ. Jyväskylä 12:1-26. 1989

MATERNAL INVESTMENT IN SEMI-DOMESTICATED REINDEER (RANGIFER T. TARANDUS L.)

Ilpo Kojola

Kojola I. 1989: Maternal investment in semi-domesticated reindeer (Rangifer t. tarandus L.). - Biol. Res. Rep. Univ. Jyväskylä 12:1-26. ISSN 0356-1062.

This paper investigates maternal investment in male and female offspring within a herd of semi-domesticated reindeer (*Rangifer tarandus tarandus* L.) in Kaamanen, Finnish Lapland (69° N, 27 ° E).

Among calves born to cows weighing less than the mean of the herd (71 kg), the proportion of males increased as maternal body weight increased. The very smallest cows (weighing less than 60 kg) gave birth to a significant excess of females. Both the medium-sized and the largest cows produced a slight, nonsignificant excess of males. The body weight of cows was closely correlated with social rank. One year delay in the age of the first reproduction brought about a tendency to compensate for the lower number of offspring with high quality males. Overall, or in any category of maternal age or weight, the sex ratio of surviving offspring did not deviate from 1:1 or from the sex ratio born.

Maternal investment for male vs. female offspring was temporally different. During gestation and the first life weeks of calf, cows invested most heavily in males. During later stages of lactation, cows rearing a male calf were able to compensate for a part of the heavier weight loss they suffered during calving. Preweaning investment in males was heavier in terms of the maternal weight change from one conception to the next. Mother's reproductive success in the subsequent year did not, however, depend on the sex of the reared calf.

During the first post-weaning winter, female calves shared a feeding site (snow crater) with their mother twice as often as male calves did. Female calves gained, in terms of the decreased weight loss, advantage from maternal social rank. However, the weight loss of mother did not depend upon the sex of the calf. Females through the age of four years showed a tendency to associate with their mother.

The results revealed in this study do not unambigiously support the hypothesis which predicts that superior females produce more male than female offspring. My results are consistent with assumption that selection will primarly eliminate the most unfit reproductive strategies. Male reproductive success is not necessarily most enhanced by an exceptionally heavy maternal investment.

Keywords: Sex ratio, maternal investment, reindeer

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This thesis is based on the following papers which will be referred by their Roman numerals:

I Kojola, I. 1989: Mother's dominance status and differential investment in reindeer calves. - Anim. Behav. 38 (in press).

II Kojola, I. 1989: Maternal investment in reindeer calves. - Submitted for publication.

III Kojola, I. 1989: Intraherd spacing behaviour of female reindeer: Effects of kinship, age, habituation and experience. - Submitted for publication.

IV Kojola, I. & Eloranta, E. 1989: Influences of maternal body weight, age and parity on sex ratio in semidomesticated reindeer (Rangifer t. tarandus). - Evolution (in press)

V Kojola, I. & Jokela, J. 1989: Sex ratio and quality of offspring in reindeer: Effects of maternal characteristics. - Manuscript.

VI Kojola, I. & Nieminen, M. 1989: Aggression and nearest neighbour distances in female reindeer during the rut. - Ethology 77: 117-124.

Contents

1. Introduction

In mammals, females typically answer for most parental care. As a result, females may have expected to have evolved reproductive "strategies" that optimize both the number and type of offspring born, as well as the level and quality of resource allocation to individual offspring (Fisher 1930, Williams 1966, Trivers 1972, Huck et al. 1986, Morris 1987).

Theoretical explanations commonly assume "trade-offs" between the intensity of reproductive effort and the parent's future reproductive potential (Williams 1966, Calow 1979, Bell 1980). Trivers (1985) has defined his original, widely quoted definition of parental investment (Trivers 1972) to "Anything done for the offspring, including building it, which increases the offspring's reproductive success at a cost to the remainder of the parent's reproductive success". Under favorable conditions, reproduction does not, however, necessarily cause detectable costs for parent's future success. Therefore, Curio (1988) has modified the latter part of the Triver's definition as follows "... the offspring's reproductive success and thereby the parent's net benefit, regardless of whether costs of reproduction exist". In any case, we may expect that parents would reach higher fitness if they are able to adjust the level and form of parental investment according to the seasonal flux in resources, their own potential and phenotype of the offspring (Morris 1985, 1987).

Iteroparous species are long-lived and they commonly have low reproductive rates. A tendency toward iteroparity balances parental investment to favor the mother's survival over that of the offspring (Eisenberg 1981). This thesis investigates maternal investment in reindeer (*Rangifer tarandus* L.), with special reference to maternal characteristics. Reindeer exhibits a female-defence polygyny (Skogland 1981, see Emlen & Oring 1977 for definition) and pronounced sexual dimorphism in size. On average, adult bulls weigh 1.7 times more than adult cows (Jarman 1983). In some populations of alpine reindeer, bulls weigh twice as much as cows (Skogland 1988). In the breeding population of a polygynous mammal, one can usually find a conconsiderable surplus of non-breeding adult males. Some longterm studies of most polygynous mammals have shown that male lifetime breeding success vary more widely than female success (Le Boeuf 1974, Clutton-Brock et al. 1982). Some theoretical explanations as well as recent empirical data sets have suggested that a sex-dependent difference in the magnitude of fitness variation influences parental strategy.

Theoretical treatment of parental investment has evoked an prediction that parents should invest more heavily in offspring of the sex among which fitness varies more widely (Trivers 1972, Trivers & Willard 1973, Maynard Smith 1980). Trivers and Willard (1973) have predicted that parents can impove their fitness by controlling the sex ratio of their offspring. Their "maternal condition hypothesis" suggests that in polygynous breeding system mothers in good condition should produce more male offspring, whilst those in poorer condition should produce more female offspring.

Polygyny is associated with predominant male dispersal (Greenwood 1980, Dobson 1982). Provided that females overtly compete for access to locally limited resources, the amount of maternal investment may be more crucial for the survival and breeding success of female than those of male offspring (Silk 1983). The resource competition model (originated by Clark 1978 and developed by Silk 1983), predicts that in those conditions dominant mothers produce more females than do subordinate mothers. This model thus contradicts the prediction of Trivers and Willard (1973).

Both the Trivers-Willard and the resource competition model are special cases of general sex allocation theory (Charnov 1982). The question of most relevant to either model is which sex shows the greatest variation in fitness as a function of mother's capacity to invest in reproduction (Meikle et al. 1984). The null hypothesis for both models could be that the determination of sex is purely a random, Mendelian phenomenon (Williams 1979).

Parents can accomplish preferential investment also by investing relatively more heavily in individual males than in individual females (Reiter et al. 1978, Trillmich 1986), or vice versa (Clark 1978, Hoogland 1981, Caley & Nudds 1987). As a result of different life-history strategies of males and females, we may expect temporal differences in maternal investment given for male vs. female offspring (Clutton-Brock et al. 1982, Silk 1988).

This thesis investigates

(1) the influence of maternal characteristics on birth sex ratio of calves (IV, V).

(2) whether survival or growth rates for male and female offspring depend differentially on maternal characteristics (II, V).

(3) whether parental investment given for male and female offspring is temporally different (I, II, III, VI).

2. Study area and animals

This study was conducted on an experimental herd of semi-domesticated reindeer (*Rangifer t. tarandus* L.) in Kaamanen, Fin-Finnish Lapland (69 ° N, 27° E). The reindeer were mostly allowed to move freely in an enclosed pasture of 70 km^2. This area comprised subalpine birch forests (*Betula pubescens*; hilltops), sparse pine forests (*Pinus silvestris*) and open fens (lower areas). Prior to calving season (May), the cows were rounded up to give birth to their calves in a 10 ha enclosure. The reindeer were provisioned with supplementary food from December to June. In 1970-1987, 1 087 calves were sexed. Most calves were weighted at birth. In 1970 and in 1976-1986, most reindeer were weighted in autumn, usually in November. A minority (10-30%) of the reindeer were measured in 1971-1975. In 1985-1986, reindeer were weighted also in the end of April and in the middle of June. Autumn weights were used as indicators of cow weight at conception and calf weight at weaning, which both take place in October. Most calves (50% of females, 85% of males) and some adults were slaughtered in autumn. Animals for slaughtering were selected by the local herders. As regards calves, those with large body sizes were slightly favored to remain in the herd. Only a few females older than nine years were retained in the herd. At this age, their reproductive success and offspring quality is clearly decreased (Eloranta & Nieminen 1986). A considerable proportion of the breeding males were transported from other Finnish herds.

3. Data collection

Data on body weights and birth dates of reindeer were extracted from the archives kept by the Association of Finnish Reindeer Herders' Cooperatives. The behaviour of reindeer was observed in 1985-1987. Definitions, observation technique and statistical methods are described in detail in original papers.

4. Results

4.1. Sex ratio

Overall, the sex ratio at birth was 51.2% males. Birth sex ratio did not deviate significantly from 1:1 in any given year (IV). In November, the proportion of males was 50.6%.

Maternal age, parity or weight change during the previous year did not significantly influence birth sex ratio of calves, whilst maternal body weight was influental (IV,V). Within all of the age categories (range 2-10 years), large-bodied cows (weighing more than the age-specific median) produced slightly more males than small-bodied cows did (IV, Table 1). The difference with offspring sex ratio between large-bodied and small-bodied cows decreased with age through the age of five years. After that age the difference increased with age (IV, see Table 1).

A more detailed analysis of the relationship between maternal body weight and offspring sex ratio showed that this dependence is nonlinear. The proportion of males increased with maternal weight only among the cows weighing less than the herd mean (71 kg) (V, Fig. 2). The very smallest cows (weighing equal or less than 60 kg) gave birth to a significant excess of female calves (IV). Sex ratios of calves born to the medium-sized or the largest cows did not deviate either from 1:1 or from each other.

Three-year old first-breeders produced more males than two-year old first-breeders did. At their first conception, three-year old first-breeders weighed 9% more than two-year old first-breeders (means of 68 and 62 kg, respectively). These females had produced more males at the age of eight years than cows which did had given birth to their first offspring at the age of two years (V).

Sex ratio of calves born to cows which did not reproduce in the previous season did not deviate from unity. However, if the calf had died not later than a month postnatally, a significant excess of males (65%) was born subsequently (IV).

The type of the previous reproductive event (male, female, no infant) influenced the type of present event more clearly among young (3-4 year old) than "middle-aged" (5-7 year old) cows (V, Table 1). The effect seemed to become stronger again as a female ages. This may be a result of tooth wear (but note small samples). The combination of male-male or female-female, produced in consecutive years, were slightly more common than the combination of male-female or female-male (IV).

4.2. Pre-weaning investment in individual offspring

Measured as the weight change of cow from one conception to the next, rearing a male to weaning had higher energetic demands on cow than rearing a female (II, Fig. 1). The frequency of reproductive failures (no infant) did not, however, significantly depend upon the sex of the calf reared to weaning in the previous year (II).

During gestation, cows invested most heavily in males. During the first life weeks of the calf, cows permitted male young to suckle more than female young (II). During the period from the middle of June to November, male-rearing cows were able to compensate for a part of the heavier weight loss they suffered during calving (II).

4.3. Offspring survivorship and growth

Of the calves born in 1976-1986, 65.2% of males and 69.3% of females survived to the slaughtering period. In any age or weight category (with the class spaces of 5 kg) of mother, the sex ratio of surviving offspring did not deviate from 1:1 or from the sex ratio born.

During the first weeks of life, male growth rate appeared to be more closely correlated with maternal body mass. Female growth rate, on the contrary, seemed to depend on maternal weight most strongly between June and November. Correlation coefficients for male and female calves did not, however, differ quite significantly (II).

Maternal body weight at conception accounted for 21% of the variation in the autumn weight of calves. The linear models provided the highest r-squares for these relationships. Corresponding figures for weights reached by offspring in their second autumn were 12% for males and 21% for females (V).

The proportional autumn weight (calf weight:cow weight) of male calves differed with the age at which their mother had initiated its reproductive life. The cows which had exhibited one-year delay with maturation, raised larger males than did cows which had given birth to their first young at the age of two years (V). Autumn weight of the female calves did not differ with mother's age at the first breeding.

4.4. Mother-offspring relationships after weaning

During the post-rut period in October, when calves are mostly weaned (Kojola unpublished data), male calves spent less time than female calves close to their mother (VI). This occured despite mature bulls were not overtly aggressive towards male calves (VI).

In experimental feeding groups which wintered in a large enclosure without provisioning, weight loss of female calves decreased as maternal social status increased. Contradicting this, the weight development of male calves did not depend on maternal rank (I). Female calves shared feeding site (snow crater) with their mother twice more often than did male calves (I). The frequency with which females fed at a crater shared with mother increased as maternal social rank increased (I, Fig. 2). The level of benefit, measured as a percentage weight loss in this connection, depended on how common this behaviour was. Only the calves of the most dominant mothers gained advantage in terms of the decline in being displaced from feeding sites by conspecifics (I, Fig. 3). This was apparently because high-status reindeer were more likely to take over a crater which was currently being used by a mother-calf pair than a crater in which a calf was feeding alone (I). Thus a further explanation was needed for to account for a positive relationship between the percentage of crater sharing and an ability to maintain body weight by female calves. Both the male and the female calves spent less time in pawing snow when they were feeding from a crater shared with their mother than when they were feeding without their mother (I, Table 4). I assume that crater sharing tend to decline the costs of foraging in calves. However, male calves exploited this option with a lower frequency than did female calves. Male calves were also found more often than female calves in the company of cow groups which did not contain their mother (I, Table 3). Weight loss of the mothers did not, however, depend upon the sex of the calf (I).

Mothers were tolerant towards their calves until subsequent calving. Provided that calves, however, had been separated from their mothers in December, they became targets of repeated rush charges by their mothers in April, after five months of separation (III). Once contacted with mother, these calves initiated to follow their mother.

In breeding parties, yearling females was located close to their mother. Maternal aggression towards them was rather uncommon (VI).

In an enclosed herd being monitored during pre-calving, the location of mother influenced the spacing behaviour of female offspring through the age of four years (III). The percentage with which mother was the nearest neighbour to female offspring decreased as the age of offspring increased (III). The weight change of mother from one conception to the next did not depend upon the existence of a yearling offspring or upon the number of female offspring present (II).

5. General discussion

The validity of Trivers & Willard's (1973) model for adaptive control of offspring sex ratio has been challenged e.g. by Myers (1978) and by Williams (1979). More recently, several empirical studies of mammals have been supportive to their "maternal condition hypothesis". Superior females have been found out to produce more males than inferior females in red deer (*Cervus elaphus*) (Clutton-Brock et al. 1981), rhesus macaques (*Macaca mulatta*) (Meikle et al. 1984), bison (*Bison bison*) (Rutberg 1986), the common opossum (*Didelphis marsupialis*) (Austad & Sunquist 1986), the golden hamster (*Mesocricetus auratus*) (Huck et al. 1986), spider monkey (*Ateles paniscus*) (McFarland Symington 1987), and mice (*Mus musculus*; Burley 1982, *M. domesticus*; Wright et al. 1988), for example. Whether these trends are adaptive or not, have been reported only in two cases. In red deer on the isle of Rhum, Scotland, only male lifetime reproductive success depends upon maternal social rank (Clutton-Brock et al. 1984). In two introduced and provisioned Caribbean island populations of rhesus macaques, estimated reproductive success of sons was more closely correlated with maternal rank than that of daughters (Meikle et al. 1984, see also Vessey & Meikle 1987).

The resource competition model (Silk 1983) contains a prediction that an extra maternal investment can be more important for lifetime reproductive success of females than that of males. In a variety of polygynous primates dominant mothers overproduce females whilst subordinate mothers overproduce males (Altmann 1980, Simpson & Simpson 1982, Silk 1983, 1988). Empirical tests with some captive primate populations have shown that female fitness depend more clearly on maternal rank than male fitness (Silk 1983, 1988). In female reindeer, competition the most favorable feeding sites can be severe during late winter (Helle 1982). As evidenced in this paper, high maternal rank is profitable to female offspring in terms of the decreased weight loss during winter. I assume that maternal rank would contribute, unlike in red deer, also in fitness of the female offspring. The sex-ratio trends revealed in this study, however, are supportive rather to the Trivers-Willard than to the resource competition model.

Available evidence for white-tailed deer (*Odocoileus virginianus*) is not supportive to the model of Trivers & Willard (1973). Well-fed white-tailed does produce more female fawns than does that are nutritionally deprived (Verme 1969, 1983). Unlike in red deer or reindeer, the litter size of white-tailed deer varies and influences the intensity of reproductive effort. The proportion of males declines as the litter size increases (Verme 1983). Caley and Nudds (1987) have, however, suggested that observed male-bias among fawns born in poor habitat is a consequence of female-female resource competition in natal groups (which makes females the more expensive sex; see Fisher 1930 for theoretical background), rather than a consequence of lowered litter size (but see McGinley 1984). The variance of male fitness should correlate positively with the degree of polygyny within the mating system (Trivers 1972, Clutton-Brock et al. 1980). As compared to white-tailed deer, red deer and reindeer exhibits a more pronounced sexual dimorphism and, seemingly, more intense male-male competition for mates (Jarman 1983, Caley & Nudds 1987). Reindeer is mostly monoparous. For these reasons we may expect that trends in the offspring sex ratio in reindeer are in accordance with the predictions derived from the model of Trivers and Willard (1973). Skogland (1986) has, however, demonstrated that more female calves are born to wild reindeer in rich than in poor habitat. The combined energetic costs due to gestation and lactation are higher than the costs merely due to the gestation (see Clutton-Brock et al. 1989). The early mortality rate of wild reindeer calves depends strongly on the availability of resources on winter ranges (Skogland 1986). In the herd studied here, the loss of a newborn brought about male-skewed sex ratio for the subsequent offspring. So far we do not however know whether this holds true for wild herds, too. Anyhow we should notice that sex ratio trends in mammals are not necessarily explained, as have been pointed out by Clutton-Brock & Iason (1986), by one adaptive theory.

As regards maternal body weight, my analysis does not unambigiously coincide with the Trivers-Willard model. The very smallest cows overproduced females as is predicted by the model. The sex ratio of calves born to the very largest cows did not, however, deviate from unity or from the sex ratio produced by the medium-sized cows. The body weight is a measure which is closely correlated with social rank (Kojola 1989). Offspring body weight was linearly related to maternal weight. Some other attributes indicative of good reproductive potential, such as fertility and offspring survival rate, are as highest among the heaviest females (Eloranta & Nieminen 1986). The apparent threshold weight below which investing in males was avoided, may support the assumption that selection primarly eliminates the most unfit reproductive strategies (see Gould & Lewontin 1979, Tuomi et al. 1983). The survival rate of calves depends on their body size (Haukioja & Salovaara 1978). My results indicate that the size reached by males at the end of the parental care is influenced by the level of maternal investment given in offspring during its first weeks of life. At this time, young are entirely dependent upon maternal resources. Males may also need more resources, simply, in order to survive (Clutton-Brock et al. 1985). In body weight, female reindeer reach an annual minimum around partution (Leader-Williams & Ricketts 1982). Calving takes place soon after a period of increased resource competition (c.f. Helle 1982) and the availability of energy is usually limited at this time. The adjustment of offspring sex ratio by starva-starvation is not adaptive (Maynard-Smith 1980). Therefore we may expect that the females which show the lowest competitive ability reach the best reproductive success by investing in female offspring.

Reproductive success of a male mammal is usually correlated with early growth rates, maternal milk yields and maternal body condition (rewieved by Clutton-Brock & Albon 1982). Helle et al. 1987) have, however, shown that at least on poor winter ranges selection for male calf size can have a stabilizing effect: small and large calves lose their fat depots sooner than the middle-sized calves do. This effect could weaken the association between maternal investment and the size reached by male offspring in adulthood (Helle et al. 1987). In principle, such a normalizing selection may influence the relationship between maternal phenotype and the sex ratio of offspring. Thus it provides a potential explanation for the nonlinearity observed.

It appeared that the age of first reproduction influences reproductive tactics of cow reindeer. As evidenced by the sex ratio of offspring and the proportional size of male calves born to cows which had delayed a year, it appears that a prolonged period for somatic investment associates with a tendency to invest most heavily in the male sex. It is attractive to explain this pattern to be a manifestation of a compensatory strategy for adverse conditions before maturation and for the consequent lowered number of offspring. We should however notice that the body weight of cows differ with the age of the first reproduction only among the first-breeders, not thisafter. Anyhow my results contradict the evidence revealed for red deer (Clutton-Brock et al. 1986) and golden hamster (Huck et al. 1986), which suggest that females showing high early growth rates would produce a male-skewed offspring sex ratio during their lifespan.

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 & Lavigne 1986, Lee & Moss 1986, Trillmich 1986, Wolff 1988). In the reindeer herd studied here, males were, measured as the weight change of mother, slightly more expensive than females to rear to weaning. If we compare the quantity of maternal investment given in male and female offspring in terms of the parent's future reproductive success (Trivers 1972, 1985), however, clear differences cannot been seen. The result deviates from that revealed for red deer on Rhum, where hinds more often fail to reproduce after rearing a male than a female (Clutton-Brock et al. 1981, see also Wolff 1988 for bison in Montana). This occurs despite male-rearing hinds have higher average rank than female-rearing hinds. The pattern observed in the Kaamanen herd coincides well with the assumption that male breeding success is not necessarily much enhanced by an exceptionally heavy investment (see Helle et al. 1987).

Maternal investment given in male vs. female offspring was temporally different. When the energy intake of offspring is most dependent on maternal resources, cows invested more heavily in male than in female offspring. At this time, mother's possibilities to influence male fitness are likely to be at their greatest. Herbivores of tundra and northern taiga have to meet the demands of short growth period and strict sesonality in the availability of resources. Short calving periods in reindeer and caribou (Bergerud 1975, Holthe 1975, Bergerud 1980, Skogland 1988) indicate that selection favors synchronization of the estruses (see also Skogland 1981). There is evidence that body condition influences the timing of conception (Skogland 1988) and also thereby influence the reproductive success in the subsequent year. Therefore male-rearing cows should be able to recover from heavier investment given in offspring during gestation and the first life weeks of young. This sets differential demands on cows investing in offspring of different sexes.

I did not found indication that post-weaning association between mother and female offspring would influence mother's body condition and thereby occur at the cost to her reproductive potential (but see Hoogland 1981, Clutton-Brock et al. 1982, Johnson 1986). My observations suggest that even sharing a snow crater with calf is not energetically expensive to the mother. The picture may, however, be different whenever snow is so hard that calves cannot dig effectively (T. Helle pers. com). By associating with their mothers, weaned female offspring learn their mother's seasonal home range (see

Clutton-Brock et 1982, Pulliainen et al. 1986). We can assume that it is likely to improve reproductive success of female offspring (Greenwood 1980). Male calves, on the contrary, may need experience primarly outside the natal group (Guinness et al. 1979).

Acknowledgements. I express my sincere thanks to Timo Helle for leading me into the behavioural ecology of reindeer and for many informal discussions thereafter. I am indebted to Rauno V. Alatalo for helpful comments on early drafts of my orginal papers. Comments made by Erkki Haukioja and Eero Helle have been profitable to this synthesis. I thank Mikko Raatikainen and Jussi Viitala for much practical and theoretical advice from the very beginning of my study. I had useful discussions with Pekka Helle, Jukka Jokela, Taina Kojola, Markku Kuitunen, Ilkka Mäkelä and Jukka Suhonen. I am grateful to Harto Linden, Mauri Nieminen, Martti Tervaniemi, Veijo Tervonen, Albin Ylisuvanto and Hannu Ylönen for providing me with working facilities. I thank Eija Eloranta, Sirpa Grekula, Marja-Liisa Kaisanlahti, Arja Kautto and Päivi Soppela for help in collecting the data. I thank Anthony Melville for checking my English. I am indebted to my parents, Ulpu and Mauri, for support and encouragement. The employees at Reindeer Research in Rovaniemi, at Konnevesi Research Station and Meltaus Game Research Station are gratefully acknowledged for their wonderful patience toward me and my intentions. The present study was financially supported by the Finnish Academy of Sciences, by the Game Foundation of Finland, by the Nordic Council for Reindeer Research (NOR) and by the Artturi and Eliel Nyyssönen Foundation.

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Selostus

Tutkimus testaa hypoteesia, joka olettaa emon panostavan voimakkaammin sitä sukupuolta edustavaan jälkeläiseen, jonka lisääntymismenestys riippuu selvemmin emän lisääntymispanostuksen voimakkuudesta. Lajeilla, joiden urokset ovat moniavioisia ja kilpailevat naaraista, emolta saatujen resurssien määrän on oletettu vaikuttavan enemmän uros- kuin naarasjälkeläisen lisääntymismenestykseen. Naarasjälkeläiset jäävät näillä lajeilla usein emänsä kanssa samaan laumaan urosten hakeutuessa jo nuorena uusille alueille. Jos naaraiden välinen resurssikilpailu on voimakasta, saattaa emän ominaisuuksilla ollakin enemmän merkitystä naaraan kuin uroksen lisääntymismenestykselle. Emät voivat periaatteessa toteuttaa voimakkaamman panostuksen toista sukupuolta edustavaan jälkeläiseen joko mukauttamalla tuottamiensa jälkeläisten sukupuolijakaumaa panostuspotentiaaliinsa tai panostamalla suhteellisesti voimakkaammin toista sukupuolta edustavaan jälkeläiseen.

Tutkimuksessa tarkasteltava aineisto on kerätty Paliskuntain yhdistyksen Kaamasen porotokasta. Tämä tokka, johon vuosina 1970 -1987 kuului vuosittain 32-93 lisääntymisikäistä porovaadinta eli noin 70 km^2:n laajuisella aidatulla alueella. Poroille annettiin lisäravintoa joulukuun ja kesäkuun välisenä aikana, muulloin ne elivät luontaisen kasvillisuuden varassa. Porot punnittiin syksyllä, tavallisesti marraskuussa. Tällöin valtaosa vasoista ja joitakin vanhimpia vaatimia teurastettiin. Porot vasoivat noin 10 ha:n laajuisessa aitauksessa, missä syntyneet vasat etsittiin päivittäin ja punnittiin. Aineisto vuosilta 1970-1987 käsittää 1 087 vasaa. Porojen käyttäytymistä tutkittiin vuosina 1985-1987.

Porovaadinten ruumiinpaino vaikutti niiden tuottamien vasojen sukupuolijakaumaan. Urosvasoja vasoneet vaatimet painoivat naarasvasan vasoneita enemmän tiinehtyessään edellissyksynä. Vaadinten ruumiinpainon ja vasojen sukupuolijakauman välisen riippuvuuden yksityiskohtaisempi tarkastelu osoitti riippuvuuden epälineaariseksi: urosvasojen suhteellinen osuus kasvoi emän painon noustessa vain keskimääräistä kevyempien vaadinten keskuudessa. Ruumiinpainon ja sosiaalisen aseman välillä oli voimakas riippuvuussuhde. Näin ollen tulos ei yksiselitteisesti tue olettamusta että voimakkaimpaan lisääntymispanokseen kykenevät emät tuottaisivat enemmän uros- kuin naarasjälkeläisiä. Pienimmille vaatimille syntyneiden vasojen merkitsevä naarasvoittoisuus näyttäisi tukevan evoluutiomallia, joka olettaa luonnonvalinnan karsivan ennen kaikkea sopimattomimmat lisääntymisstrategiat. Vaatimen iän vaikutus vasojen sukupuolijakaumaan oli vähäisempi kuin ruumiin painon. Vastasyntyneen vasansa menettäneille vaatimille seuraavana keväänä syntyneiden vasojen sukupuolijakauma oli merkitsevästi urosvoittoinen. Kolmevuotiaina lisääntymisensä aloittaneet vaatimet tuottivat suhteellisesti enemmän uroksia kuin kaksivuotiaina aloittaneet. Näiden vaadinten tuottamat urosvasat olivat painavampia kuin kaksivuotiaina aloittaneiden. Syksyyn saakka elossa säilyneiden vasojen sukupuolijakauma ei eronnut missään emon ikä- tai painoluokassa merkitsevästi tasajakaumasta tai ko. luokassa syntyneiden vasojen sukupuolijakaumasta. Emän paino selitti sekä uros- että naarasvasojen syyspainosta 21%. Tämä riippuvuussuhde oli lineaarinen.

Emät panostivat urosjälkeläisiin naarasjälkeläisiä voimakkaammin kantoaikana. Urosvasat painoivat syntyessään 6% naarasvasoja enemmän ja emät menettivät keskimäärin enemmän painostaan vasoesssaan uros- kuin naarasvasan. Vastatakseen urosvasojen suurempaan energiantarpeeseen ne sallivat urosvasojen imeä naarasvasoja enemmän ensimmäisten vasontaa seuraavien viikkojen aikana. Urosvasoja hoitaneet emät pystyivät osittain palautumaan vasonta-aikana syntyneestä painonmenetyksestä ennen syksyä. Vaikka urosvasan hoitaminen vierotusikään olikin emän painonmuutoksella mitattuna merkitsevästi "kalliimpaa" kuin naarasvasan hoitaminen, ei emän lisääntymisen onnistuminen seuraavana vuonna riippunut hoidetun vasan sukupuolesta. Tulos tukee olettamusta että poikkeuksellisen voimakas panostus urosjälkeläiseen ei välttämättä ole kannattavampaa kuin keskimääräinen panostus. Lyhyt kasvukausi asettaa vasonnan ajoittumiselle tiukat rajat. Urosvasoja tuottavien emien on kyettävä tehokkaasti kuntoutumaan, jotta ne voisivat lisääntyä onnistuneesti myös seuraavana vuonna.

Vieroitusta seuraavan talven aikana naarasvasat ruokailivat emänsä kanssa samalla kaivukuopalla yli kaksi kertaa yleisemmin kuin urosvasat. Kaivukuopan jakaminen yleistyi emän sosiaalisen aseman kasvaessa. Naarasvasojen talvinen painonmenetys vähentyi emän sosiaalisen aseman kasvaessa. Vaikka naarasvasat näin hyötyivät emänsä asemasta, emän painonmenetys talvella ei riippunut vasan sukupuolesta. Ainakaan helpohkoissa lumiolosuhteissa kaivukuopan jakaminen ei näytä olevan suoranaista vieroituksen jälkeistä panostusta vasaan. Naarasjälkeläiset seurailivat emojaan ainakin nelivuotiaiksi asti. Vierotettujen naarasjälkeläisten lukumäärällä ei ollut vaikusta emän lisääntymispotentiaaliin.