THE POTENTIAL FOR MULTIPLE FECUNDITY OF MOOSE IN FINLAND

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ABSTRACT: Multiple fecundity (i.e., >2 fetuses or calves per female) is a rare and poorly known phenomenon in moose (*Alces alces*). In this paper I: (1) report the frequency of multiple fecundity of moose in Finland; (2) study the frequencies of multiple fecundity in different years and areas; (3) discuss the viability of litters with different numbers of progeny; and (4) discuss the possible fecundity effects of selective harvest and the evolutionary aspects of multiple fecundity. The embryo numbers of harvested cows were counted during 1980-89 (*n* = 2,347) and the proportion of single, twin, and triplet calves were determined from the 1986-99 moose observation material recorded in the field by hunters during the hunting season (*n* = 585,149). The material includes 4 sets of quadruplet calves, 1 set of stillborn sextuplets, and a moose female with 5 sets of triplet calves; a total of 30 calves in 15 years. In Finland, 60.38 % of pregnant moose cows had one, 39.37% two, 0.21% three, and 0.04% four embryos. In the observation material, 61.79% of the cows had one calf, 38.18% twin calves, and 0.03% triplet calves. The proportion of multiple cases decreased from south to north. The viability of single and twin calves was found to be very high, but only 15% of the sets of triplet calves seemed to survive up to the first fall. Calf survival rate was clearly higher in 1980-99 than in 1963-66, possibly depending on the different age structures of the female populations. According to the literature, the frequency of multiple fecundity in moose appears to be lower in North American than European moose populations.

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Key words: *Alces alces*, calf survival, fecundity, moose, multiple fecundity, quadruplet calves, reproduction, sextuplet calves, triplet calves, twinning

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In favorable conditions, the reproductive potential of a moose (*Alces alces*) population can be very high (Markgren 1969, Stålfelt 1974, Nygrén 1983, Cederlund and Sand 1991, Danilkin and Ulitin 1998, Schwartz 1998). Most females annually produce either single or twin calves. The non-reproducers are pubescent females (1-2 years old), very old cows (15-20 years), or females unable to give birth every year while living on the poor forage or harsh conditions of the North (Peek 1962, Blood 1974, Markgren 1974, Albright and Keith 1987). The most productive females can give birth to as many as 3 (Peterson 1955, Heptner et al. 1966, Danilkin 1999) or 4 calves (Skuncke 1949, Knorre 1959, Ling 1974, Martin 1989, Vitakova and Minajev 2000).

In different moose populations the proportion of singles and twins varies (Markgren 1969, Mech et al. 1987, Boer 1992, Gasaway et al. 1992, Danilkin and Ulitin 1998, Schwartz 1998) but in all moose populations multiple fecundity (i.e., >2 fetuses or calves per single moose female) is a very rare phenomenon (Pimlott 1959, Heptner et al. 1966, Franzmann 1981, Kozlo 1983, Schwartz 1998). In addition, the number of reports of triplet or quadruplet sets is small (Table 1) and analytical papers dealing with the maximal productivity of moose are practically nonexistent. Ling (1974) and Kozlo (1983) might be the only authors who report

Table 1. Reports of multiple fecundity cases in female moose (*Alces alces*).

Region[1]	Method[2]	Sample Size[3]	Number Of Triplets	% Triplets	Number Of Quadruplets	Author
NA	1	-	+	-	-	Seton (1927) cited by Peterson (1955)
NA, Alaska	1	-	1	-	-	Hosley and Glaser (1952)
NA, Ontario	1	-	3	-	-	Peterson (1955)
NA, Newfoundland	3	1,579	2	0.13	-	Pimlott (1959)
NA, Isle Royale	1	-	1	-	-	Moll and Moll (1976) cited by Martin (1989)
NA, Alaska	3	3,314	2	0.06	-	Bailey and Bangs (1980)
NA, Alaska	1	-	1	-	-	Franzmann (1981)
NA, Alaska	3	-	1	-	-	Franzmann and Schwartz (1985)
NA, Isle Royale	1	-	1	-	1	Martin (1989)
RU	1	-	1	-	-	Buturlin (1890) cited by Timofejeva (1974)
RU, Komi	2	-	>2	-	1	Knorre (1959)
RU, Tatarskij	2	-	3	-	-	Zaripov and Znamenskiji (1964) cited by Heruvimov (1969)
RU, Leningrad	2	2,139	4	0.19	-	Dementev (1967) cited by Ling (1974)
RU, Kirov	2	-	1	-	-	Pavlov and Jazan (1967) cited by Timofejeva (1974)
RU, Vladimir	2	58	1	1.72	-	Sysojev (1967) cited by Ling (1974)
RU Moscow	3	248	1	0.40	-	Makarova (1969) cited by Ling (1974)
RU Tambov	2a	141	2	1.42	-	Heruvimov (1969)
RU, Leningrad	2	1,850	4	0.22	-	Novikov (1970) cited by Ling (1974)
RU, Novosibirsk	2	358	1	0.28	-	Zinovjev (1971) cited by Danilkin (1999)
RU, Volga	2	54	1	1.85	-	Jazan (1972)
RU, Leningrad	2	3,364	4	0.12	-	Timofejeva (1974)
RU, Byelorussia	2a	190	3	1.58	-	Kozlo (1983)
RU, Murmansk	2	1,209	1	0.08	-	Makarova (1981)
RU, Arkhangel	2	678	2	0.29	-	Filonov (1983)
RU, Vologda	2	2,416	3	0.12	-	Filonov (1983)
RU, Tver	2	1,726	1	0.06	-	Filonov (1983)
RU, Jaroslavl	2	1,312	2	0.15	-	Filonov (1983)
RU, Moscow	2	2,826	1	0.04	-	Filonov (1983)
RU, Kaluga	2	627	2	0.32	-	Zaikin and Voronin (1986) cited by Danilkin (1999)

RU, Kirov	2a	327	3	0.92	-	Glushkov (1987)
RU, Komi farm	4	230	1	0.43	-	Kozhuhov (1989)
RU, Chernozemje	2	2,040	2	0.10	-	Prostakov (1996) cited by Danilkin (1999)
RU, Kostroma farm	4	315	9	2.86	1	Vitakova and Minajev (2000)
BC, Estonia	3	6,721	60	0.89	16	Ling (1974)
BC, Estonia	2a	67	-	-	1	Kirk and Tönisson (1994)
BC, Estonia	1	-	>4	-	-	Kirk and Tönisson (2000)
BC, Estonia	2a	114	2	1.75	-	Kirk (2001)
SC, Sweden	2	-	+	-	-	Lönnberg (1923)
SC, Sweden	1	-	9	-	1	Skuncke (1949)
SC, Finland	2a	402	3	0.75	-	Koivisto and Rajakoski (1966)
SC, Norway	1	-	2	-	-	Ling (1974)

[1] NA = North America, RU = Russia, BC = Baltic Countries, SC = Fennoscandia.

[2] 1 = random observations, 2 = fetuses, determined by hunters, 2a = fetuses, determined by scientists, 3 = cow-calf observations, 4 = calves born on moose farms.

[3] Pregnant females or cow-calf observations.

and also analyze triplet or quadruplet observations or frequencies.

The purpose of this paper is to: (1) report the frequency of multiple fecundity of moose in Finland from 1980 to 1999; (2) study the spatial and temporal variation of the frequency of multiple fecundity and the effects of environmental and geographical factors; (3) study the viability of litters with different numbers of progeny; (4) discuss the possible fecundity effects of selective harvest and evolutionary aspects of multiple fecundity; and (5) discuss possible differences in multiple fecundity of European and North American moose populations.

STUDY AREA

The study area was the whole of Finland. Finland mainly belongs to the boreal forest or taiga region, but is situated 500-1,000 km further to the north than boreal forests elsewhere. In Fennoscandia, the vegetation is boreal but the light conditions are arctic (Solantie 2001). The typical vegetation types in Finland are coniferous forests (70%) and mires (30%). Approximately 50% of the forests are pine (*Pinus* spp.) dominated, 30% spruce (*Picea* spp.) dominated, and 7% birch (*Betula* spp.) dominated. Since the 1950s, artificial forest regeneration with pine plantations throughout Finland has dramatically increased the amount of moose forage, but at the same time, it has restricted the distribution of other forage species. In Finland, all boreal vegetation zones are represented (Fig. 1).

The bedrock of northern and eastern Finland (Lapland, Oulu, Kainuu, and Pohjois-Karjala) is mainly composed of ancient, nutrient-poor rock. The bedrock is more fertile in the southwestern part of Finland. The terrain of Finland is quite flat and the total area of lakes constitutes approximately 10% of the land surface. Due to the strong effect of the sea, the climate is moist. The winters are not as cold as in other boreal

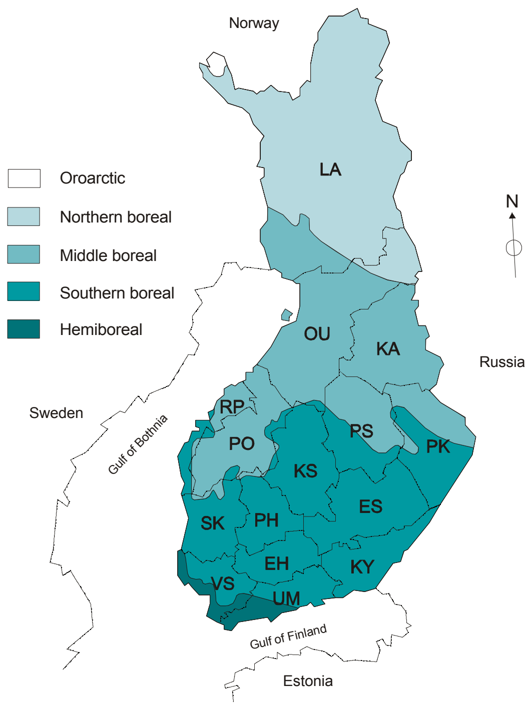

Fig.1. Vegetation zones and Game management districts of the study area in Finland.

areas. There are 110 snow-days per year in the hemi-boreal area and 200 days around the border of the central and northern boreal zones. The deepest snow layer (long-term average in March > 60 cm, 30-year maximum 90-120 cm) and the mostly continental climate is typical for the districts of Pohjois-Karjala, Kainuu, Oulu, and Lapland where a small number of large predators exist and take their share of the moose population. In these areas (except Lapland), moose are the only numerous ungulate prey for brown bear (*Ursus arctos*) and wolf (*Canis lupus*). In coastal Finland, the seasons are less pronounced, the climate is more windy and humid, and the snow depth is lower (long-term average < 30 cm, 30-year maximum 60-80 cm).

Data were collected in 15 game management districts: Etelä-Häme (EH), Etelä-Savo (ES), Kainuu (KA), Keski-Suomi (KS), Kymi (KY), Lapland (LA), Oulu (OU), Pohjanmaa (PO), Pohjois-Häme (PH), Pohjois-Karjala (PK), Pohjois-Savo (PS), Ruotsinkielinen Pohjanmaa (RP), Satakunta (SK), Uusimaa (UM), and Varsinais-Suomi (VS). The districts were grouped into 4 regions: Coastal Finland (EH, KY, UM, VS, SK, and RP), Inland Finland (ES, KS, PH, PO, PK, and PS), Oulu (KA and OU), and Lapland (LA) (Figs. 1 and 2). The administrative divisions of the data were based on the established practices of moose management in Finland. The division into regions was based on vegetation zones, the position/distance from the coastline, and comparative calculations and long-term observations of the spatial characteristics of the moose population (Nygrén and Pesonen, Finnish Game and Fisheries Research Institute, unpublished data).

In 1981-96, the estimated numbers in the winter moose population in the study area were between 67,000 and 93,000; the number of annual moose kills was between 26,000 and 69,000, and the average percentage of kill in the total population was 39% (T. Nygrén and Pesonen 1989; Nygrén 1996; T. Nygrén, Finnish Game and Fisheries Research Institute, unpublished data).

METHODS

The Finnish Game and Fisheries Research Institute (FGFRI) collected data with the aid of Finnish hunters as part of the Finnish moose research program. The program has been conducted mainly for management purposes since 1972. Two types of data and samples were used.

Reproductive Organs of Pregnant Females

The reproductive organs of female moose were collected during the hunting seasons of 1980, 1984, 1985, and 1989. In 1980 and 1985, the collection area was the whole of Finland (Fig. 2); in 1984, the samples were collected from a 5,617-km^2 area in the western part of the Oulu management

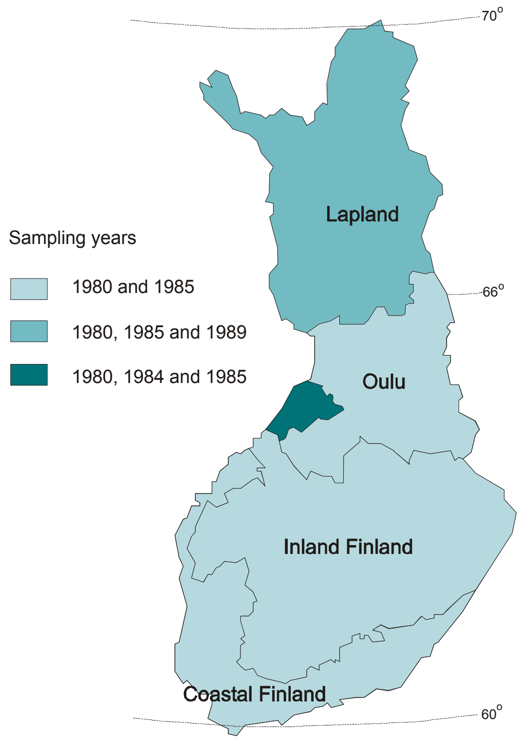

Fig.2. Sampling areas and regions of Finland used in the study.

district and in 1989, from the Lapland game management district (Fig. 2). In 1980, 1985, and 1989, the moose kills in Coastal and Inland Finland were between 15 October and 15 December, and in Oulu and Lapland regions between 1 October and 15 December. In 1984, the samples were collected during an exceptional winter hunt between 14 January and 31 January. Specimens of genitalia and jaws were also collected. The hunting teams were advised to take random samples from adult (> 1 year old) females and to send them as quickly as possible to the FGFRI Ilomantsi Game Research Station by mail. No preservative or freezing was used. In most cases, the material arrived in good condition within 1-4 days after the kill. The samples included ovaries, uteruses, vaginas, and, to determine age, jawbones or front teeth. Information about the date and place of kill, sex, carcass weight (weighed, estimated, or both), as well as information about lactation and possible calves following or killed with the mother was included. The organ samples were studied and measured and the numbers and measurements of the embryos/fetuses were determined. All triplet and quadruplet cases were photographed. The ages of the females were determined by Matson's Lab in Montana, USA, using cementum annuli. The viability of single, twin, and triplet embryos were determined by comparing the embryo numbers with the numbers of single, twin, and triplet calves in the moose observation data.

Moose Observations

Since 1976, moose observations have formed the most important source of information for moose management in Finland. Each hunting day, the hunting teams classify observed moose as bulls, cows without calves, cows with 1 calf, cows with 2 calves, or as unidentified animals. The teams are advised to record the observed animals on a card once a day, even if they were seen many times or by many hunters during the day. Usually, hunters give additional information if they have made an unusual observation of triplet calves or killed some or all of them. When the hunting season is over, the teams mark the estimated number of moose still living in the hunting area on the observation card. The completed observation card is sent to the Ilomantsi FGFRI by mail. In 1986-99, the average annual number of cards totaled about 4,300 and the average number of moose observations exceeded 201,000. The average coverage of the returned cards was 83% (the coverage % is the proportion of licenses allowed to the hunting teams). The frequency of cows with 1, 2, or 3 calves was determined annually and regionally from the observation data. In addition, the average weights of killed male and female triplet calves was determined and compared with the long-term average weights of killed moose calves

(Nygrén and Pesonen 1989).

Additional information about unusually large litters was also given by mail or by phone to the Ilomantsi FGFRI. The reliability of this information was carefully checked before the results were included in the data set. Among them were reports about the triplet mother "Elli", 3 sets of quadruplets, and a set of stillborn sextuplets.

RESULTS

Multiple Pregnancies in Finland

In the data from 2,347 uteri of pregnant moose, 5 included triplets and 1 had quadruplet embryos (Table 2). Four out of the five triplet sets were found in Inland Finland and one in Coastal Finland (Table 2, Fig. 3). The only quadruplet set was found in Lapland. Two triplet sets were recorded in 1980 and three triplet sets were recorded in 1985 (Table 2). No triplet or quadruplet sets were found in 1984 and 1989.

Case studies of triplets and quadruplets:

1. An 8.5-year-old cow (EH 2267/80) was killed on 2 November 1980 (Fig. 3). The lengths of the embryos were 24 mm, 23 mm, and 24 mm, respectively.
2. An 8.5-year-old cow (KS 803/80) was killed on 16 November 1980 (Fig. 3). The embryo lengths were 82, 78, and 75 mm, respectively. Three primary yellow bodies existed in the right ovary.
3. A 9.5-year-old cow (ES 4207/85) was killed on 15 October 1985 (Fig. 3). The cow had milk in its udder. The estimated carcass weight was 230 kg. The lengths of embryos were 4 mm; 3 primary yellow bodies were found in the ovaries.
4. A 9.5-year-old cow (ES 2945/85) was killed on 20 October 1985 (Fig. 3). It did not have milk. The measured carcass weight was 175 kg. The embryo lengths were 16 mm, 6 mm, and 17 mm, respectively. One of the embryos had died before the cow was killed and its amnion was twisted around the axis. All 3 primary yellow bodies were in the right

Table 2. Proportions of pregnant female moose (*Alces alces*) with 1-4 embryos in utero, collected from different areas of Finland between 1980 and 1989.

Area/Year	Number of uteri	Number of embryos in utero							
		1		2		3		4	
		n	%	*n*	%	*n*	%	*n*	%
Coastal Finland	922	561	60.85	360	39.05	1	0.11		
Inland Finland	931	510	54.78	417	44.79	4	0.43		
Oulu	186	119	63.98	67	36.02				
Lapland	308	227	73.70	80	25.97			1	0.33
1980	749	461	61.55	286	38.18	2	0.27		
1984	67	49	73.13	18	26.87				
1985	1,248	698	55.93	547	43.83	3	0.24		
1989	283	209	73.85	73	25.80			1	0.35
Finland 1980-89	2,347	1,417	60.38	924	39.37	5	0.21	1	0.04

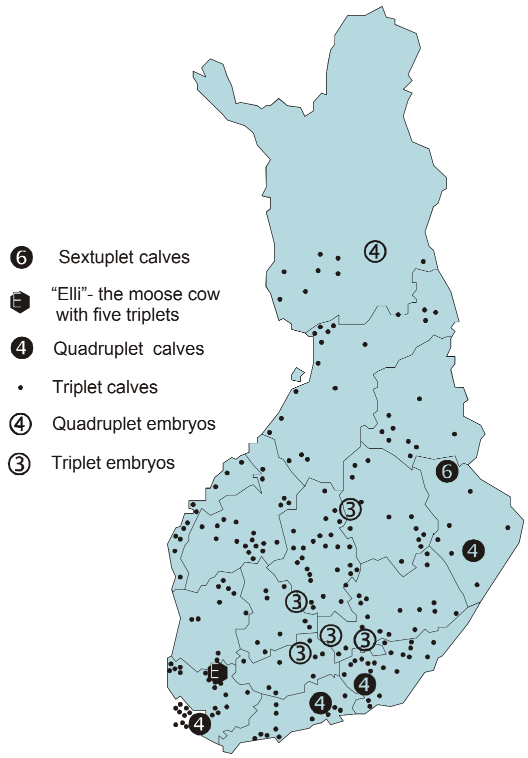

Fig.3. Locations of multiple fecundity cases in Finland, 1980-2001.

ovary.

5. A 12.5-year-old cow (PS 4961/85) was killed on 3 November 1985 (Fig. 3). It had milk and the estimated carcass weight was 215 kg. The embryo lengths were 13 mm, 11 mm, and 13 mm, respectively. Two embryos (13 and 11 mm) were in the left horn and one in the right horn (13 mm). The membranes in the left horn were tightly together. The membranes of the smaller embryo were twisted around the main axis, and the amount of fluid was small. The embryo itself seemed to be in good condition. Only 2 primary yellow bodies existed, both in the left ovary. Quite obviously, the embryos in the left horn were single-egg twins.
6. An un-aged cow (LA 958/89) was killed on 3 November 1989 (Fig. 3). The estimated dressed weight was 175 kg. The cow had milk and a male calf was following it (dressed weight 78 kg). The calf was killed just before its mother. The embryo lengths were 36 mm, 33 mm, 35 mm, and 34 mm, respectively. There were 2 primary yellow bodies in both ovaries.

Triplet Observations in the Field

The 585,149 calf-cow observations collected in 1986-99 included 191 triplet cows (0.033 %). The annual number of triplets varied between 1 (0.003%) and 28 (0.047%) (Table 3). The triplet degree correlated significantly with the twinning degree annually ($r = 0.605$, df = 12, $P = 0.022$; Fig. 4) and an apparent 4-year cycle of twinning and triplet rate was found in 1988-99 when annual twin and triplet frequencies were compared (Fig. 5).

In the game management districts, the triplet frequencies varied between 0.014% (Lapland) and 0.071% (Varsinais-Suomi) (Table 4). The frequencies were highest in Coastal Finland and decreased gradually to the North. The degree of twins and triplets was indicative of spatial correlation ($r = 0.462$, df = 13, $P = 0.083$; Fig. 6).

An interesting case was the triplet mother "Elli" (Figs. 3 and 7). This moose cow, with a smaller than average head, was easy to identify. She was a yearling without

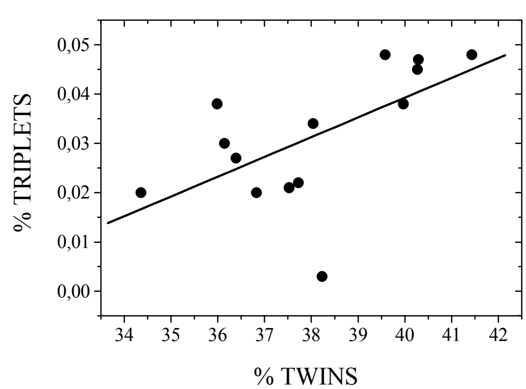

Fig.4. Correlation of annual twin and triplet frequencies in Finland, 1986-99 ($R = 0.605$, df = 12, $P = 0.022$).

Table 3. Annual proportions of single, twin, and triplet moose (*Alces alces*) cow-calf observations in Finland, 1986-99.

	Cows with 1 calf		Cows with 2 calves		Cows with 3 calves		Total cow-calf observations
Year	*n*	%	*n*	%	*n*	%	*n*
1986	19,546	62.248	11,847	37.729	7	0.022	31,400
1987	21,412	61.761	13,256	38.236	1	0.003	34,669
1988	25,328	63.151	14,771	36.829	8	0.020	40,107
1989	28,334	63.580	16,218	36.393	12	0.027	44,564
1990	26,953	61.927	16,556	38.039	15	0.034	43,524
1991	25,226	59.993	16,806	39.969	16	0.038	42,048
1992	26,757	62.449	16,080	37.530	9	0.021	42,846
1993	28,939	63.971	16,282	35.992	17	0.038	45,238
1994	27,722	59.687	18,703	40.268	21	0.045	46,446
1995	25,678	63.826	14,541	36.144	12	0.030	40,231
1996	22,756	65.619	11,916	34.361	7	0.020	34,679
1997	21,559	60.371	14,135	39.582	17	0.048	35,711
1998	25,474	58.515	18,039	41.437	21	0.048	43,534
1999	35,890	59.665	24,235	40.289	28	0.047	60,153
Total	361,574	61.792	223,385	38.176	191	0.033	585,150

Fig.5. The 4-year cycle in twin and triplet frequencies in Finland, 1986-99.

calves in 1989. During her life span "Elli" gave birth to 5 sets of triplets and 30 calves (Table 5). Because of a protection decision by hunters, only 6 of its offspring were killed as calves. "Elli's" family lived throughout the years in a territory of 1,200 ha. Often the family foraged in local gardens. If disturbed, "Elli" protected her calves with exceptional violence. Almost all triplets were strong and similar-sized. The carcass weight of the single calf killed in 2000 was 114 kg - significantly over the 83 kg average carcasss weight of Finnish moose calves in the fall. In 1999, at the age of 11.5 years, "Elli" gave birth to her last triplet set. One of the calves, especially well-protected by the mother, was much smaller than the others were. In 2002 "Elli" gave birth to twins, was aging rapidly and limped with her hind leg. The last calf was born in 2003, probably prematurely, because the hunters never saw any calf that summer. "Elli" herself was finished at the age of 15 years on 14th July 2003 after the joint decision of hunters and scientists. She was very weak, carcass weight was 111 kg. Hardly any fat was found in her organs, but her teeth were in

Table 4. Proportions of single, twin, and triplet moose (*Alces alces*) cow-calf observations in different areas of Finland, 1986-99.

Game management District/Area	Cows with 1 calf		Cows with 2 calves		Cows with 3 calves		Total cow-calf observations
	n	%	*n*	%	*n*	%	*n*
Etelä-Häme	12,837	62.276	7,768	37.685	8	0.039	20,613
Kymi	19,401	62.083	11,830	37.856	19	0.061	31,250
Ruotsink. Pohjanmaa	17,249	58.680	12,139	41.296	7	0.024	29,395
Satakunta	20,056	60.966	12,831	39.004	10	0.030	32,897
Uusimaa	18,714	60.440	12,237	39.521	12	0.039	30,963
Varsinais-Suomi	17,729	57.063	13,318	42.866	22	0.071	31,069
Coastal Finland	105,986	60.155	70.123	39.800	78	0.044	176,187
Etelä-Savo	26,521	59.714	17,877	40.252	15	0.034	44,413
Keski-Suomi	31,225	60.838	20,074	39.112	26	0.051	51,325
Pohjanmaa	26,507	57.311	19,725	42.648	19	0.041	46,251
Pohjois-Häme	13,937	63.046	8,162	36.922	7	0.032	22,106
Pohjois-Karjala	21,992	63.126	12,840	36.856	6	0.017	34,838
Pohjois-Savo	25,566	56.351	19,793	43.627	10	0.022	45,369
Inland Finland	145,748	59.659	98,471	40.307	83	0.034	244,302
Kainuu	26,129	65.349	13,846	34.629	9	0.023	39,984
Oulu	47,498	64.861	25,719	35.120	14	0.019	73,231
Oulu	73,627	65.033	39,565	34.947	23	0.020	113,21 5
Lapland	36,213	70.390	15,226	29.596	7	0.014	51,446
Finland	361,574	61.792	223,385	38.176	191	0.033	585,150

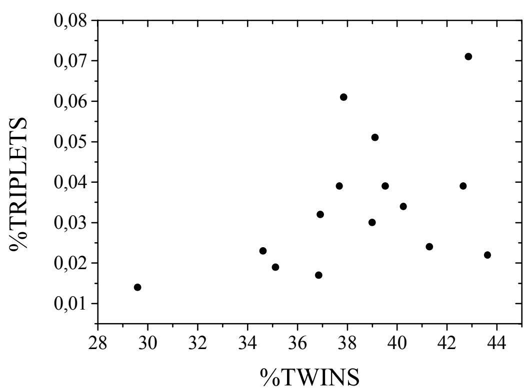

Fig. 6. Correlation of twin and triplet frequencies in different areas of Finland, 1986-99 (R = 0.462, df = 13, P = 0.083).

good condition. Under the skin was found hundreds of lead pellets. One of the pellets had caused the chronic inflammation in the hip joint of the right leg. Also parasitic pneumonia was diagnosed and very high concentrations of cadmium were found in her liver and kidneys, but lead concentrations were low.

Quadruplet Observations

Four quadruplet observations have been documented in Finland: 1 in 1957 (Anon 1957) and 3 in 2000 (Fig. 3). In 1957, only 1 calf lived more than 1 week. In 2000, the

Fig.7. Moose female "Elli" with her triplet calves (photo: Vesa Mustonen 1995-96).

Table 5. Annual calving history of "Elli", a female moose (*Alces alces*) from Coastal Finland.

Year	"Elli's" age (years)	Number of calves born	Number of calves killed
1988	0	0	
1989	1	0	
1990	2	2	2
1991	3	2	2
1992	4	2	1
1993	5	3	0
1994	6	2	0
1995	7	3	0
1996	8	3	0
1997	9	3	0
1998	10	2	0
1999	11	3	0
2000	12	1	1
2001	13	1	0
2002	14	2	0
2003	15[1]	1[2]	0
Total		30	6

[1]died 14th July.

[2]probably prematurely born, determined by inspection of "Elli's" genitalia.

viability of 2 litters could be followed through the summer and in both cases only 3 of the 4 calves survived until the hunting season. In the third case, the quadruplet calves were observed for the first time in September and no further observations were made during the hunting season.

In three of the documented quadruplet cases, the size-difference of the calves was clear. In 1957, the total weights of the 3 dead quadruplets were 4.7, 7.0, and 9.5 kg. In 2000, one of the quadruplets was much smaller and weaker than the others were in 2 of the 3 observed cases of that year. Only the quadruplets observed in September were all of similar size but they were much smaller than average moose calves during that time of the year.

Premature Birth of Sextuplets

On 18 May 2001, a calving place of 6 premature moose calves was checked (Fig. 3). One stillborn calf lay at one end of the calving ground and 5 at the other end. According to the condition of the carcasses, the birth had taken place about 1 week earlier. The weights of the calves were 4.0

kg (female), 3.8 kg (male), 3.5 kg (male), 3.3 kg (male), 2.7 kg (male), and 2.5 kg (female). The two smallest calves PK 1013/01 and PK 1014/01 (Fig. 8) had died some weeks earlier in the uterus. Vague signs of respiration were evident only in the male calf of 3.3 kg (PK 1012/01).

Survival of Multiple Fetuses and Calves

The proportion of early triplet embryo sets in the data was 0.21%, but the proportion of triplet calves observed in fall was only 0.03% (Fig. 9). According to this, the viability of triplet embryos is quite low. Only about 15% of triplet embryo sets seem to be complete up to the age of 6 months. The viability of quadruplets is probably even lower.

Compared with the survival rate of triplet and quadruplet sets, the survival rate of single and twin embryos to the age of 6 months seems to be very high (Fig. 9). From the early embryonic period to the age of 6 months, the proportion of singles increased in the total data by 2.4%. The proportion of twin pairs decreased by 3.0%, while the proportions of triplet sets decreased by 85.5% and quadruplet sets by 100%. Consecutively, from embryos in 1985 until calves in 1986, the figures were: singles +11.3%, twin pairs –13.9%, and triplet sets –90.8%. Multiple calves obviously have an insignificant effect on calf productivity per fertile female (Table 6).

Carcass Weights of Triplets

The average carcass weight of triplets killed during the hunting period was 72.0 kg. The annual averages varied between 58.5 and 78.9 kg. For male triplets, the average weight was 74.9 kg (n = 62), and for female triplets 69.3 kg (n = 62). The carcass weights of female triplets varied between 37 and 100 kg and for male triplets between 41 and 106 kg.

DISCUSSION

Kozlo (1983) expressed strong doubt about the viability of triplet embryos. No definite evidence was available at the time that the triplet or quadruplet sets were observed to ensure they were the offspring of one moose female only. Later Kozhuhov (1989) as well as Vitakova and Minajev (2000) reported that in farming conditions, 9 viable triplet sets and 1 quadruplet set were

Fig. 8. The stillborn sextuplets found on 18 May 2001 in Nurmes, Finland (photo: Tuire Nygrén).

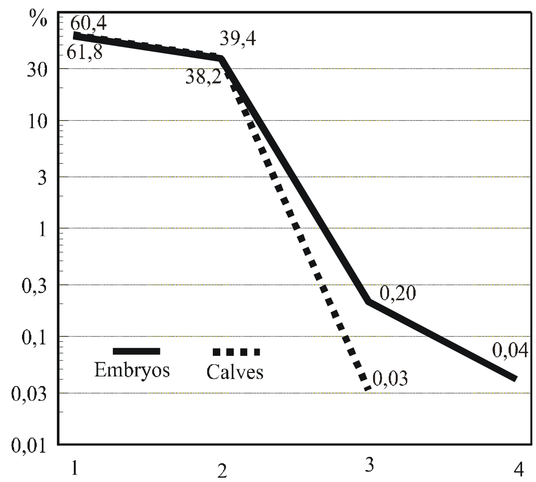

Fig.9. Proportions of single, twin, triplet, and quadruplet litters of embryos and calves in Finland.

born. Most of the farmed triplets had, however, low birth weight and their death rate was high (Kozhuhov 1989). In this study, I have shown that multiple births also occur in nature and some triplet sets even survive until the next autumn. "Elli", the 15 year-old cow moose, gave birth to 5 sets of triplets, 6 pairs of twins, and 3 single calves, and brought most of its 30 calves to adulthood. On the Kostroma farm in Russia, one of the most productive moose females, "Alysha", had given birth to triplets once at the age of 13 years (Kozhuhov 1989). Altogether, "Alysha" had been pregnant 14 times and given birth to 26 calves.

The present material includes 1 triplet embryo set with only 2 yellow bodies in the ovaries of the cow. Koivisto and Rajakoski (1966), Markgren (1969), as well as Kirk and Tõnisson (1999) have also reported cases of identical twins as a part of triplet embryo sets. Obviously monozygotic twins are a normal, but rare event, in the European moose.

In this study, 0.21% of the pregnant females had triplet embryos. About 20 years earlier, Koivisto and Rajakoski (1966) found 0.75% triplet embryos in the same area ($n = 402$). Heruvimov (1969) reported 1.42% triplet embryos in the Tambov region of Russia ($n = 141$), Kozlo (1983) 1.58% in Byelorussia ($n = 190$), and Kirk (2001) 1.75% in Estonia ($n = 114$). The frequencies of triplets in the former Soviet Union are often much higher than those observed in Finland. This is consistent with the finding that the frequency of triplets decreases towards the north (South and Central Russia 0.28-1.69%, North Russia 0.04-0.22%) as reviewed by Danilov (1987).

In the surveys based on the information provided by Russian hunters, the frequencies of triplet embryo sets varied from 0 to 1.72%. In reports with at least 1 triplet set observation, the average frequency of triplets was 0.14% (Table 1). Compared with the specialists´ results of embryo numbers, these lower frequencies were predictable. As, for example, Timofejeva (1974) has pointed out, the skills of the hunters seldom are good enough to reliably count the embryo numbers in the uteri during early fall.

Table 6. Number of embryos per pregnant moose (*Alces alces*) cow and calves per calf-cow in Finland.

Area	*n*	Embryos/pregnant cow	*n*	Calves/calf-cow
Coastal Finland	922	1.39	176,190	1.40
Inland Finland	931	1.46	244,301	1.40
Oulu	186	1.36	113,215	1.35
Lapland	308	1.27	51,446	1.30

In most studied populations, the proportion of multiple fecundity cases has been zero but sometimes, in favorable conditions and/or in reports based on small sample sizes, the percentage of triplet embryos has been higher than 2%. In farming conditions, Vitakova and Minajev (2000) reported 2.20% triplets and 0.24% quadruplets (*n* = 409). Most probably, if all studied natural populations were included, the proportion of triplet embryo sets of European moose would vary between 0 and 1%.

The overall percentage of triplet calf observations in fall was 0.03% in my material (*n* = 585,149). Twenty years earlier Koivisto (1963) reported not a single triplet cow in Finland (*n* = 39,818). Makarova (1969 cited by Ling 1974) reported 1 triplet set (0.40%) in the Moscow region (*n* = 248). Ling (1974) reported 60 cases of triplets (0.89%) in Estonia (*n* = 6,721). As expected, the triplet calf frequencies are lower than the triplet embryo frequencies. In the present material, triplet calf frequencies were highest in Southwest Finland and lowest in Lapland (Table 3). This is also consistent with the earlier result that the number of multiple fecundity cases is less frequent in the North than in the South (Danilov 1987).

The opportunities to compare the temporal change of multiple fecundity frequencies are very few. Koivisto and Rajakoski (1966) found 3 triplets (0.75%) in the uteri of 402 pregnant moose females. The twinning percentage was 49.8%. In this study, the proportion of triplet embryos was 0.21% and with twin embryos, it was 39.4%. However, the proportion of twin calves in fall was lower in 1963-65 (24.7%) (Koivisto 1963) than in 1980-99 (38.2%). During 1963-65, all triplet sets and about 50% of twin pairs had been lost before the fall. In 1980-89, all of the quadruplet sets, 85% of the triplet sets, but only 3% of twin pairs, were lost from the population before the fall. The difference is considerable and hardly can be explained by the difference in methods. The most probable explanation is the differences of the age structure of female populations. In 1963-65, the average age of harvested females was 3.3 years (*n* = 1,075) and only 6.3% of the killed females were ≥ 7 years old (Koivisto, FGFRI, unpublished). In the 1997-99 material (*n* = 2,584), the average age was 4.3 years and 19.5% of females were ≥ 7 years old (Nygrén et al. 1999; T. Nygrén, FGFRI, unpublished). According to Glushkov (1987, 1991), the calves of older, experienced females survive better than the calves of young females. Older females usually give birth earlier than younger ones and the earlier calves have a higher probability of surviving until or during the following winter (Ericsson and Wallin 1999, Keech et al. 2000).

Ericsson and Wallin (1999) and Testa et al. (2000) found no significant difference in the survival rate of twin and single moose calves. My results, as well the results of Glushkov (1987, 1991), are the opposite, but according to Glushkov's age-structured material (1987, 1991), the mortality rate of triplets, twins, and singletons in Northeast Russia was significantly higher than in Finland. All triplet sets and 82% of twin pairs were eliminated from the population before the first fall and the proportion of singletons increased by 8%. In the younger age classes (< 6 years), the elimination frequencies were higher than in the older age classes. Compared with Glushkov's results (1987, 1991) and, for example, Osborne (1991) and Ballard et al. (1991), the viability prognosis for twin pairs (3% decrease in frequency) and singletons (2% increase in frequency) in Finland is high. A multitude of factors probably lie behind these differences; at least the larger populations of large predators in Russia and North America as well the different age structure of populations explain some of the difference in calf survival.

The average carcass weight of the harvested triplets was 11 kg lower than the average overall carcass weight (83 kg) of moose calves in Finland (Nygrén and Pesonen 1989). The difference was 12.7 kg for female and 9.1 kg for male calves. At the time of birth, the normal weight of Finnish moose calves is about 8-13 kg (T. Nygrén, FGFRI, unpublished). Calves with a weight less than 7-8 kg are seldom viable (Heptner et al. 1966). This also seems to be the case in North America, where the maximum fetal mass of a cow moose is, according to Geist (1974), nearly 23 kg. The upper limit of the total weight of the fetuses of European moose is unknown. However, if we assume that the total weight of normal twins is about 16-26 kg, we can calculate that a strong adult female could give birth to 3 viable 7 kg calves but for most females, 4 calves of this minimum size would be too much. At least this appeared to be the case with the observed quadruplet sets. None of these survived until the first fall. In 1957, only one survived; the dead calves weighed 4.7 kg, 7.0 kg, and 9.5 kg.

According to the embryo numbers per pregnant female and the calf numbers per calf-rearing cow, the potential for reproduction is highest in Inland Finland and lowest in Lapland. The differences in female age structure (Nygrén 1999) can explain most of the spatial productivity differences existing; in the North, there are more young females without a calf than in the South, but in both areas, fertile females seem to be very capable to rear their calves to the first fall. In the North, no signs of higher calf losses were found. Knowing the harsh climate of the North, the result remains unexpected.

Compared with the mortality of Russian and North American moose, the total natural mortality of moose is low in Finland. Excluding hunting mortality, the average annual mortality of moose (both adults and calves) has been estimated at approximately 3% (T. Nygrén, FGFRI, unpublished). Usually, only during severe winters with deep snow (> 1 m) and a dense moose population (4-8 moose/1,000 ha of land area) a few dead yearlings are found in Southern Finland in April-May. More regularly, dead calves and yearlings are found in Northern Finland, but even there the numbers are comparatively low. In Sweden, with substantially higher moose densities than in Finland but with almost similar natural and hunting conditions, Cederlund and Sand (1991) estimated that the natural mortality of calves was no higher than 1%. The low death rate of moose calves in Finland also gained support from a helicopter survey conducted by Heikkinen (1998). He found that calves comprised 50.7% of the total number of moose in February-March 1998 in a 1,600 km^2 sample area where the observed proportion of calves had been 48.4% two to three months earlier at the end of the hunting season in 1997 (T. Nygrén, FGFRI, unpublished). Obviously, the natural calf mortality of the present moose population of Finland is very low: the population of large predators is small, the amount and quality of forage is high, and, as a result of selective hunting, the population structure is very productive and the proportion of experienced females high.

The triplet frequencies in Finland were highest in those areas with the highest calf production; the frequencies decreased towards east and north where the twinning degree has permanently been lower (Nygrén et al. 2000). The spatial correlation between the twin and triplet frequencies was close to significant and the temporal correlation was significant. Earlier, Ling (1974) found a significant correlation between the frequencies of twins and triplets in Estonia. Later Kirk (2001) also reported high frequencies of multiple pregnancies in Estonia. Ling's survey methods (i.e., hunters' observations) have been criticized (e.g., Kozlo 1983) because the number of triplet and quadruplet observations was much higher than in all previous reports (Table 1). The main point raised by the critics was the possibility that orphan calves join with strange calf-rearing cows and thus cause false observations of triplet or even quadruplet sets. However, moose research in Finland from 1971 to 1999 has not recorded a single case of moose females accepting orphan calves. On the contrary, there are numerous examples of aggression rather than normal agonistic behavior between calf-cows and other moose (K. Nygrén, FGFRI, personal communication). Therefore, I find it quite possible that Ling's result (1974) was sound.

The existing correlation between twin and triplet frequencies is consistent with the assumption that multiple fecundity is an extreme case of twinning. When the hereditary potential for productivity is high, the age structure optimal, and the living conditions favorable for reproduction and survival, the frequencies of twinning and multiple fecundity cases tend to increase. The most important critical factors seem to be: (1) low population densities compared with the carrying capacity of the feeding grounds; (2) weak or nonexistent populations of large predators; (3) mild winter conditions and cool, humid summers; and (4) an age structure with a high frequency of females at their best reproductive age. All these factors existed in Finland during the survey.

According to a theory by Geist (1974), cows conceiving twins or even triplets are favored in the rapidly expanding but slowly contracting moose habitats where forage is seasonally superabundant and the long daylight hours of the Northern summer permit carbohydrate accumulation and a greater rate of milk production. When resources are marginal, single calves are favored. Geist theorizes that there must be mandatory selection for high reproductive rates in expanding populations of moose, favoring the evolution of twinning. He also thinks that under conditions of favorable forage availability and quality it can be expected that natural selection will act against cow moose bearing single calves, which can grow too large and chance dystocia. I have no record of such delivery difficulties as recorded for caribou (Bergerud, personal communication, according to Geist 1974) and find the selection against cow moose bearing single calves not very probable – not at least in Finnish circumstances. The living conditions are favorable. The heavily hunted populations are in a constant state of expansion (without any real increase in population numbers). The twin-rearing cows are better protected than the cows without calves and single-calf cows by legislation and selective hunting recommendations. As a result, the success of twin cows and twin and multiple calves to survive and reproduce remains high, and the frequency of genes for higher reproductive potential can slowly increase.

The number of multiple fecundity reports is much larger in the European than in the North American literature. There are several possible reasons behind the difference. The first is the modern research methods, which seldom allow a sufficiently numerous sample size (Schwartz 1998). This could explain the small amount of multiple fecundity cases reported in North America. The second possible reason is a lower probability to make calf-cow observations in North America, where hunting takes place closer to roads with smaller hunting teams. In Finland, big moose hunting teams (Koskela and Nygrén 2002) use vast areas with a very dense road network. The third possibility is that the reported difference between multiple fecundity cases in Europe and North America is real, as has been speculated by Geist (1998). Perhaps the small number of multiple embryo and calf observations in North America is a result of a genetic difference in reproductive potential compared to European moose populations. No direct evidence is available on the matter, but it would be unjustified to exclude the possibility of hereditary differences in multiple fecundity between the area with 68 chromosomes (Gustavson and Sundt 1968) in Europe and the area with 70 chromosomes (Wurster and Benirscke 1967) to the east of Yenisei River in Russia and in North America (Boeskorov 1997).

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