A STUDY OF *ELAPHOSTRONGYLUS ALCES* IN AN ISLAND MOOSE POPULATION WITH LOW CALF BODY WEIGHTS

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ABSTRACT: We studied prevalence of *Elaphostrongylus alces* (Protostrongylidae; Nematoda), weights, mandible lengths, and mandible marrow fat in a moose population (*Alces alces*) at Utö in the Stockholm archipelago from October 1989 to November 1994. The moose population at Utö before culling was relatively dense (2.0/km^2). Annual prevalence of infection with *E. alces* (adult worms, and /or eggs/larvae in meninges) varied between 58% and 71%. The moose calves at Utö were smaller (mandible length 294±18 mm, n = 73) and had lower processed carcass weights (45.4±10.4 kg, n = 85), (bled, without viscera, skin, skull, and lower legs) than calves on the mainland. Low weights could not be statistically related to infection with *E. alces*, nor were there indications that low calf weights were related to lack of browse. However culling of moose calves and yearlings over a three year period resulted in a trend of reduced infection with *E. alces*. In a total of 2025 snails and slugs examined over 5 summers, 20 (1 %) were infected with elaphostrongyline larvae. Seven species (*Arion subfuscus*, *Deroceras agreste*, *D. reticulatum*, *Limax cinereoniger*, *Succinea* spp., *Vitrina pellucida*, and *Zonitoides nitidus*) were found naturally infected, with a mean of 4.3±5.2 larvae/gastropod. *Succinea* spp. was the most abundant gastropod, and together with *Deroceras agreste*, *D. reticulatum*, and *Arion subfuscus* was the most probable source of *E. alces* infection. Further study is required to follow and evaluate the effects of the culling on *E. alces* as well as on the moose population at Utö.

ALCES VOL. 31 (1995) pp.61-75

Body mass is an important biological parameter. Weight data provide information about growth rates and regional variation in growth. Also, information about body size, reproduction, and variation in life strategies can be related to body mass (Saether and Haagenrud 1983, 1985, Saether 1985, Langvatn and Albon 1986, Saether and Heim 1993, Langvatn 1995).

For several consecutive years, unusually small moose calves were observed at Utö , in the Stockholm archipelago (59°N, 18°15'E). Overall moose density on Utö was estimated by aerial survey in 1984 to be 2.0/km^2 but the effective moose density was greater since nearly 50% of the island consists of bare rock or poorly developed vegetation. In the 1988 hunting season, the average processed carcass weight of 8 calves shot in October was 39 kg (bled and without viscera, skull, skin and lower legs). We sampled moose calves and yearlings shot in the 1989 hunting season, and found lower weights, and poorer nutritional status than in animals on the mainland. We also found heavy infection with *Elaphostrongylus alces*, a nematode parasite which can cause cerebrospinal nematodiasis.

Elaphostrongylus spp. are parasites found in and around the spinal cord as well as in muscle fasciae, of cervids. Eggs and larvae initiate an inflammatory response but adults do not (Stéen and Rehbinder 1986, Stéen 1991). Eggs and/or first-stage larvae (L1) are thought to pass via the blood and lymphatic system to the lungs of cervids and are coughed up, swallowed and excreted with the feces (Panin 1964, Mason 1989). They then invade a gastropod and develop to the infective third stage (L3) (Demiaszkiewicz 1987). Cervids probably ingest infected gastropods accidentally, after which larvae develop to the adult stage that is found in the epidural space of the spinal cord and in muscle fasciae (Hemmingsen 1986, Stéen 1991). Infection with *Elapho-strongylus* spp. in cervids can cause ataxia and paresis, resulting in difficulties in foraging, decline in condition, starvation, and finally death (Halvorsen 1986, Stéen 1991). Stuve (1986) reported that adult moose ($\geq$2 years) in Norway infected with *Elaphostrongylus* were of lower weight than uninfected moose.

The production of *E. alces* larvae is age dependent with the number of L1's decreasing in older moose (Stuve 1986, M. Stéen unpubl. data). Animals older than 5 years of age do not pass larvae (Stuve 1986), in contrast to *E. rangiferi* in reindeer in which the number of larvae passed increases up to the age of 6 years, and remains high in older animals (Halvorsen *et al.* 1985, Halvorsen 1986). Consequently, changing the age structure of a moose population, by reducing the number of young animals that produce more larvae, could reduce the level of *E. alces* infection.

The objectives of the present study were to determine 1) which gastropods served as intermediate hosts for *E. alces* at Utö, 2) if low calf weights were correlated with *E. alces* infection, 3) if the prevalence and intensity of *E. alces* infection can be reduced, by changing the age structure of the moose population, 4) if the moose calves at Utö were smaller in body size and weight than those on other islands and the mainland, as well as to 5) estimate moose population density, and 6) estimate abundance and utilization of moose browse.

STUDY AREA

Data were collected at Utö (23.86 km^2) (Fig. 1), and two neighbouring islands, Ålö

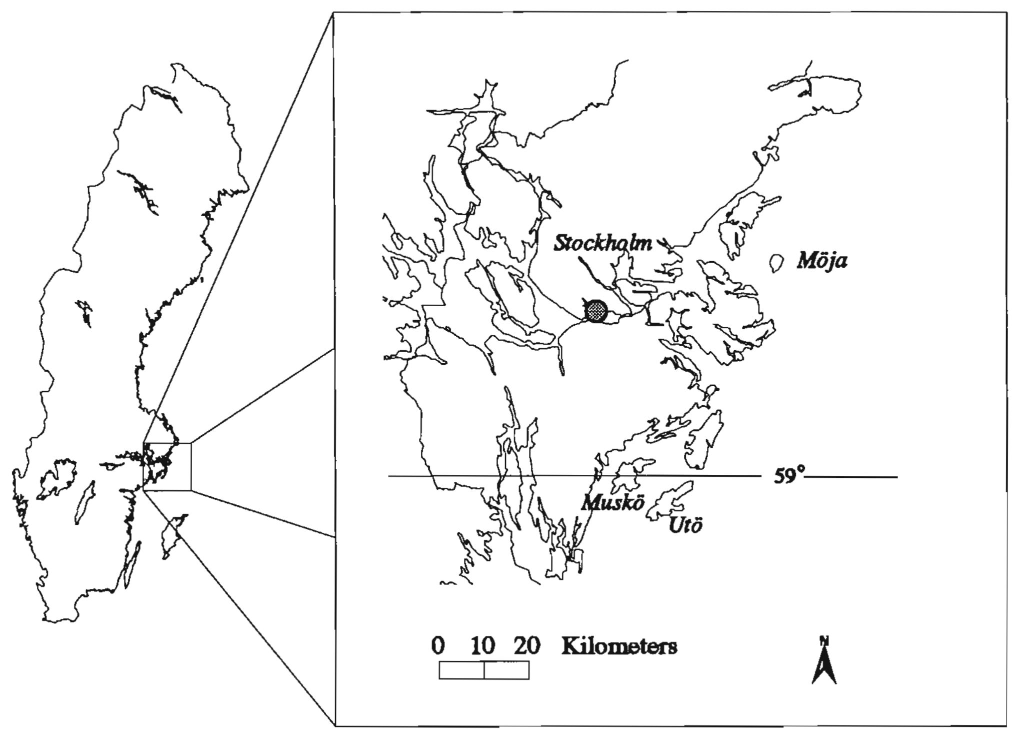

Fig. 1. Map showing the location of Utö, Muskö and Möja, Sweden.

(5.57 km^2), and Rånö(5.86 km^2). All three will be referred to collectively as Utö.

The islands consist of nearly 50% bare rock and poorly developed vegetation, the remainder is mixed coniferous-deciduous forest. The mean annual precipitation from 1985 to 1990 was 433 mm, and the mean annual temperature from 1961 to 1990 was 6.1 C, measured at Utö and Stabbö weather stations (Alexandersson *et al.* 1991). The maximum altitude is 40 m above sea level. The only cervids on the islands were moose and roe deer (*Capreolus capreolus*). No large predators were present.

For comparison, data were also collected from two additional islands, Muskö, 6-7 km west of Utö and closer to the mainland, and Möja, about 50 km north-northeast of Utö. Both are similar in size and habitat to Utö.

METHODS

E. Alces in Intermediate Hosts

Snails and slugs were sampled on the southern part of the island of Utö in the periods June - September 1990, May - October 1991 and 1992, May and July - September 1993 as well as June and August 1994. Eighteen plots (10 x 12 m) were established in areas utilized by moose cows with calves and in biotopes where gastropods could be anticipated. A 2 x 10 m section of each plot was searched every month, for a period of one hour. Litter on the ground and vegetation up to eye-level were examined for gastropods. Snails and slugs were identified to species (Kerney *et al.* 1979) and examined for elaphostrongyline larvae by compressing their tissue between two glass slides and examining them using a compound microscope at x40 magnification. Larvae were identified according to morphology and dimensions given by Demiaszkiewicz (1986).

E. Alces in Moose

All moose calves shot during a 3 year period at Utö from 7 October, 1990 to 29 January, 1991 (90/91), 19 October, 1991 to 23 March, 1992 (91/92), and 24 October, to 30 December, 1992 (92/93) were examined for *E. alces*. The vertebral column, head, lungs, and feces were collected. The material was kept frozen at -20 C until examined. Lungs and feces were examined for dorsal-spined larvae. Material was suspended over cheesecloth in funnels (10 cm top-diameter) filled with tap water using a modified Baermann technique (Baermann 1917). The head and vertebral column were cut along the mid-line with a band saw while still frozen. Lateral nerves were cut and each half of the spinal cord was removed. The surface of the dura mater and the adjacent epidural space were examined. The brain, including the dura and pia-arachnoid, was also examined. The number of adult *E. alces* found was recorded as none (n=0), few (1-3), moderate (4-10), or many (>10). The brain, spinal cord and meninges were fixed in 10% formalin. Histological specimens were processed, cut at a thickness of 4 µm and stained with haematoxylin and eosin. The presence of egg and/or larvae, the extent of inflammation (negative, mild, moderate, strong) and the type of inflammatory response (none, acute, subacute, chronic) in the meninges of the spinal cord were determined from histological samples. Calves were classified as infected when adult *E. alces* were found and/or eggs/larvae were observed in sections of spinal cord.

Body Weight, Growth and Condition

Data were collected during fall over a 6 year period between October 1989 and November 1994. Moose were shot at Utö 9 October, 1989 to 26 February, 1990 (89/90), 90/91, 91/92, 92/93 (dates given in the previous section), 25 October, to 26 November, 1993 (93/94), and 29 October, to 2 November, 1994 (94/95). During the hunting seasons of 90/91, 91/92, and 92/93, local hunters were directed to eliminate calves and yearlings. During the remaining hunting seasons (89/90, 93/94, and 94/95), hunters culled moose that were judged to be small, regardless of age.

Processed carcass weight of all moose was recorded. Mandibles were collected and stored frozen (-20 C) until analyzed. Age was determined by tooth eruption and wear (Skunke, 1949) and by cementum annuli (Reimers and Nordby 1968). Body size was estimated by total mandible length (Langvatn 1977). Body condition was estimated by mandible marrow fat (Cederlund *et al.* 1986) and by visual judgement of the epidural fat in the vertebral column (two categories, good and poor; calves only).

On the islands of Muskö and Möja weights and mandibles were obtained during fall hunting 15 October to 7 December, 1990 (90/91), 19 October to 23 October, 1991 (91/92), and 16 October to 22 October 1993 (93/94). The material was treated as described for Utö.

Population Density - Availability and Utilisation of Browse

A plot survey technique was used on the islands of Utö during the period 21 to 23 April, 1993. Sampling points (n=405) were established at 150 m intervals along transect lines (n=26) spaced 500 m apart. Around each sampling point, three circular plots of different size were demarcated: 1) an approx. 300 m^2 plot (r=10 m; radius estimated) to describe the habitat, 2) a 100 m^2 plot (r=5.64 m) to count moose pellet groups and 3) a 20 m^2 plot (r=2.52 m) to estimate available browse and browsing pressure.

Habitat was described as either forest, bog, marsh, beach, impediment or other (*i.e.* roads, plots around houses, gravel pits). Community type was described according to dominant tree species: Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), mixed conifers, mixed conifers and deciduous, and deciduous, and forest stand according to age (0-2, 3-10, 11-20, 21-40, and 41+ years).

Pellet groups from the previous winter were counted within the 100 m^2 plots. Groups with at least 20 pellets and with the mid-point of the group within the border of the plot were counted. Age of pellets was estimated from their colour and position in relation to litter and vegetation. The length of the winter was defined as the period from the mid-date of the birch leaf-fall (*Betula* spp.; 17th October) and the mid-date for the survey (22 April). Defecation rate was based on 14 pellet groups/day (R. Bergström, pers. communication).

Available browse within the 20 m^2 plots was estimated as percent cover occupied by woody species within 0.3-3.0 m of the ground (Skogsstyrelsen 1991). Accumulated browsing pressure was estimated in four classes (none=0, weak=1, moderate=2, heavy=3) from the architecture of the tree, *i. e.* the amount of change in normal growth form thought to be caused by browsing over the life-time of the tree. Previous winter´s browsing was estimated by using the percentage of last season´s shoots which were browsed (Skogsstyrelsen 1991). Browsing classes used were: none (=0 %), weak (<10 %), moderate (10-50 %) and heavy (>50 %). The level of use of each tree species was calculated as the mean value of the given codes for accumulated browse, and the mean value of the class median (none=0%, weak=5%, moderate=30%, and heavy=75%) for previous winter's browse.

Statistics

Weights, mandible lengths and marrow fat, were evaluated by analysis of variance (ANOVA), followed by Fishers Protected Least Significant Difference statistic for mean comparisons. Means were tested against each other only if significance was found in the ANOVA. Differences in condition and levels of *E. alces* infection between years were evaluated by Chi-square-test. The Mann-Whitney U-test was applied to establish if weights of uninfected and infected calves differed. To avoid the effect of weight loss during winter (Schwartz *et al.* 1984), only data collected from 7 October to 4 December, 1990, 1991, and 1992 were used. Differences were considered non-significant if $p > 0.05$. Mean values available in the published literature were compared to our results by *t*-test.

RESULTS

E. Alces in Intermediate Hosts

The 2,025 terrestrial gastropods (68% snails, 32% slugs) sampled from 1990 to 1994 consisted of 18 species of snails and 12 species of slugs (Table 1). *Succinea* spp. were the most common snail (48%) and provided the greatest number of infected individuals. *Deroceras laeve* was the most common slug (27%); however, none was infected.

Elaphostrongyline larvae were found in 7 different species at an over-all annual prevalence of 1.8%, 0.4%, 0.5%, 1.0%, and 2.6% from 1990 to 1994, respectively. The mean number of larvae per infected gastropod was 4.3± 5.2. Eight of the 20 infected gastropods had only one larva; a maximum of 20 larvae was found in one slug (Table 2). No infected gastropods were found in May. The mean monthly temperature was >10 C when gastropods were collected except the months of October, 1990; May and October, 1991; October, 1992 and 1993; when it was colder.

When the humidity was high, *Succinea*

Table 1. Terrestrial gastropods examined for elaphostrongylinae larvae at Utö.

Species	1990	1991	1992	1993	1994	Total
Slugs						
Arion subfuscus	18 (0)[1]	36 (1)	9 (0)	5 (0)	10 (2)	68 (3)
Deroceras agreste	15 (0)	25 (2)	6 (0)	4 (0)	15 (0)	65 (2)
D. reticulatum	16 (0)	42 (0)	1 (0)	1 (0)	1 (1)	61 (1)
Limax cinereoniger	2 (1)	7 (0)	3 (2)	1 (0)	1 (0)	14 (3)
Uninfected slugs[2]	99 (0)	220 (0)	29 (0)	74 (0)	15 (0)	447 (0)
Snails						
Succinea spp.	70 (3)	272 (0)	162 (0)	108 (3)	46 (2)	658 (8)
Vitrina pellucida	21 (2)	30 (0)	2 (0)	0 (0)	1 (0)	54 (2)
Zonitoides nitidus	38 (1)	36 (0)	103 (0)	43 (0)	21 (0)	241 (1)
Uninfected snails[3]	114 (0)	97 (0)	54 (0)	72 (0)	80 (0)	417 (0)
Total	393 (7)	765 (3)	369 (2)	308 (3)	190 (5)	2025 (20)

1) Number examined followed in brackets by number infected.

2) Uninfected slugs: *Arion ater* (total n=129), *A. circumscriptus* (26), *A. fasciatus*(30), *A. hortensis* (2), *A. intermedius* (38), *A. silvaticus* (18), *Deroceras laeve* (175), and *Limax tenellus* (19).

3) Unifected snails: *Bradybaena fruticum* (total n=70), *Carychium minimum* (1), *Cepea hortensis* (112), *Clausilia cruciata* (1), *C. bidentata* (6), *Cochliocopa lubrica* (40), *Cochlodina laminata* (1), *Columella* spp. (35), *Discus ruderatus* (2), *Ena obscura* (2), *Euconulus alderi* (15), *E. fulvus* (24), *Nesovitrea hammonis* (94), *N. petronella* (9), and *Oxychilus alliarus* (5).

Table 2. Number and developmental stage of elaphostrongyline larvae found in terrestrial gastropods at Utö May to October, 1990 to 1994.

Species	June	July	Aug.	Sept.	Oct.
Slugs					
Arion subfuscus	1(4 L3)[1]	-	-	-	1(1 L1)
	1(7 L3)				
Deroceras agreste	1 pos.[2]	-	-	-	1(1 L2, 1 L3)
D. reticulatum	1(20 L3)	-	-	-	-
Limax cinereoniger	-	1(1 L3)	-	1(2 L2)	-
	-	1(2 L3)	-	-	-
Snails					
Succinea spp.	1(11 L2)	3(1 L2)	1(3L1, 10L2)	1(6 L3)	-
		1(1 L3)			
		1(3 L3)			
Vitrina pellucida	-	-	-	2(1 L1)	-
Zonitoides nitidus	1(4 L2-L3)	-	-	-	-

1) Number infected (number of larvae and developmental stage; L1 = first stage larvae, L2 = second stage larvae, L3 = third stage larvae).

2) No information on number or stages of larvae.

spp. were frequently found on leaves from 0.2 m to 1.5 m above ground level. *Deroceras* spp. also moved to higher levels (0.2 - 1.0 m above the ground) when the weather was damp. The Arionidae were more frequently found on lower ground vegetation. *Limax cinereoniger* and *Zonitoides nitidus* were found only on or in the ground litter.

E. Alces in Moose

Of 57 calves (28 females, 29 males), the prevalence of adult *E. alces* was 67% in 90/91 and 91/92, and 58% in 92/93 (Table 3). The intensity of infection with adult *E. alces* did not differ significantly among years (x^2= 0.993, p= 0.91, "moderate" and "many" categories were pooled), although no animal with >10 worms was found in 92/93.

The prevalence of eggs and/or larvae in the meninges did not differ in calves among the 3 years (33%, 9.5%, and 25%, respectively, x^2 = 3.65, p=0.16), nor did the extent of meningeal inflammation seen in infected animals (x^2 = 9.19, p=0.16). There was, however, a trend toward a milder reaction (17 % rated negative and 17% strong in 90/91 compared to 50% negative and 8.3% strong in 92/93. The type of inflammatory response also changed over the 3 years; fewer animals were categorized as subacute/chronic and more had either no or acute inflammation (x^2= 11.21, p = 0.024, subacute and chronic were pooled) (Table 4).

The prevalence of calves classified as infected with *E. alces* (adult worms, and/or eggs/larvae in meninges) did not differ among years (71% in 90/91, and 91/92, 58% in 92/93, x^2 = 0.72, p=0.70).

There was no significant difference among years between dorsal-spined larvae

Table 3. Intensity of adult *E. alces* in 57 moose calves shot at Utö.

	Intensity[1]				Total	
Year	None	Few	Moderate	Many	exam.	% inf.
90/91	8 (33.3)[2]	4 (16.7)	9 (37.5)	3 (12.5)	24	67.0
91/92	7 (33.3)	4 (19.0)	8 (38.1)	2 (9.5)	21	67.0
92/93	5 (41.7)	3 (25.0)	4 (33.3)	0 (0)	12	58.0

1)See text for details.

2)Number infected (% of total examined that year)

Table 4. Type of inflammatory reponse (%) in the meninges of 57 moose calves shot at Utö.

Year	n	No inflammation	Acute	Subacute	Chronic
90/91	24	16.7[1]	8.3	54.2	20.8
91/92	21	9.5	28.6	42.9	19.0
92/93	12	50.0	16.7	33.3	0.0

1) Percentage of total animals sampled that year judged to have an inflammatory response in the following categories: No inflammation; Acute = presence of oedema, macrophages, neutrophiles; Subacute = presence of mononucleate leukocytes, no oedema; Chronic = presence of organized mononucleate leukocytes, active proliferation and encapsulation by connective tissue.

per gram (LPG) lung and feces. The prevalence of dorsal-spined larvae in lungs of the 57 calves was 70%, 58%, and 64% (x^2 = 0.618, p = 0.73) in 90/91, 91/92, 92/93, respectively; the median number of larvae per gram (LPG) of lung tissue was 24(max.=294), 6(180), and 8(46); the prevalence of larvae in feces was 60%, 64%, and 50%, (x^2 = 0.547, p = 0.76); and the median number of LPG of feces was 20(max.=174), 3(79), and 2(41), respectively.

The mean carcass weight of calves shot on Utö 7 October to 4 December 1990-92 infected with *E. alces* (n=33) did not differ from that of uninfected (n=15) calves (Mann-Whitney U-test, Z=-0.523, p=0.6012) (Table 5).

Moose on the island of Muskö had adult *E. alces* in the vertebral canal and dorsal-spined larvae in feces (2 of 9 examined). Those on Möja were passing dorsal-spined larvae (2 of 8 samples) but their identity was not confirmed.

Body Weight, Growth and Condition

A total of 170 animals (105 calves, 14 yearlings and 51 moose ≥2 years) was shot during the study; 82 females and 88 males. Of these, 131 were harvested at Utö (Table 6), 18 at Muskö, and 21 at Möja.

Mean calf weight at Utö was 45.4±10.4 kg, at Muskö 48.3±7.4 kg and at Möja 65.4± 8.2 kg (Table 7). Overall, male calves were heavier than female calves (F = 6.941, p = 0.0097), and thus the sexes were separated for further analysis. Calf weights differed among the three islands ($F_{females}$ = 8.204, p = 0.0009; F_{males} = 11.987, p = 0.0001); calves

Table 5. Processed carcass weights (kg) of moose calves, with and without *Elaphostrongylus alces* infection, shot at Utö, 7 October to 4 December, 1990-92.

	Uninfected					Infected with *E. alces*				
Year	n	x̄	S.D	min	max	n	x̄	S.D	min	max
1990	6	44.8	8.7	32	55	13	47.4	10.6	25	61
1991	4	44.5	12.3	27	54	14	42.7	13.5	22	73
1992	5	53.0	5.4	48	62	6	52.2	9.2	39	67
Total	15					33				

Table 6. Moose shot at Utö during the hunting season from 89/90 to 94/95.

Year	Calves	Yearlings	≥2 years	Total
89/90	15	4	12	31
90/91	24	3	1	28
91/92	21	0	6	27
92/93	12	1	5	18
93/94	9	1	8	18
94/95	4	1	4	9

at Möja were heavier than on the other two islands (mean comparison test). The mean weights of calves sampled on Utö did not differ over the five year sampling period, although extremely low weights (< 35 kg) were not recorded at Utö after 91/92 (Fig 2).

The mean weights of yearlings and ≥2-year-old animals did not differ among Utö, Muskö, and Möja (F= 0.89, p= 0.44, and F=1.68, p=0.20, respectively), nor did the weights of females and males differ in either of these older age groups (F = 0.889, p = 0.4386, and F = 1,679, p = 0.1973, respectively).

Mandible length of calves (Table 8) differed significantly among islands (F = 3.28, p = 0.042); those at Möja were longer than at Muskö (mean comparison test). The length of mandibles did not differ between the sexes for any age group (calves F=2.71, p=0.1036;

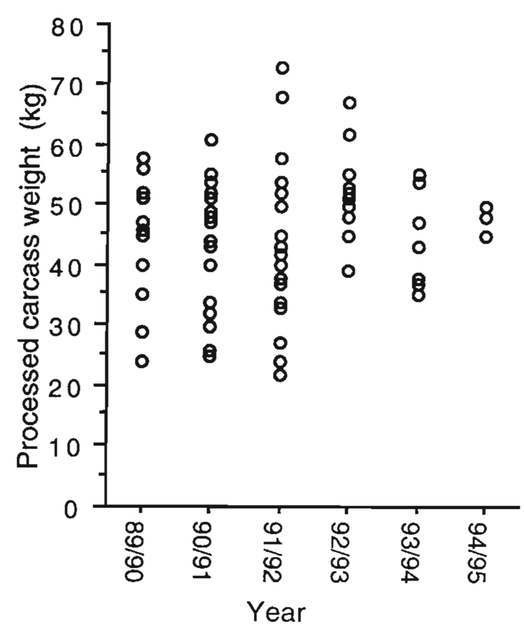

Fig. 2. Processed carcass weights of calves shot at Utö 89/90 to 94/95.

Table 7. Mean processed carcass weights (kg) of moose shot at Utö, Muskö, and Möja 1989-94.

		Mean processed weight [1]		
Area	Age group	Overall	Females	Males
Utö	Calves	45.4±10.4[2c]	42.8±10.2[ac]	47.9±10.2[bc]
		(22-73)(85)	(22-67)(42)	(24-73)(43)
	Yearlings	112.6±23.3[e]	104.5±25.1[e]	118.0±22.5[e]
		(74-145)(10)	(74-132)(4)	(80-145)(6)
	≥2 years	149.8±31.6[f]	143.9±26.7[f]	159.0±37.2[f]
		(90-236)(36)	(91-208)(22)	(90-236)(14)
Muskö	Calves	48.3±7.4[c]	43.8±7.5[ac]	52.0±5.3[bc]
		(35-60)(9)	(35-50)(4)	(48-60)(5)
	Yearlings	137.0±44.6[e]	-	137.0±44.6[e]
		(94-183)(3)	(0)	(94-183)(3)
	≥2 years	162.7±50.4[f]	160.0±2.8[f]	164.0±65.0[f]
		(106-246)(6)	(158-162)(2)	(106-246)(4)
Möja	Calves	65.6±8.2[d]	61.4±5.2[ad]	68.8±9.2[bd]
		(57-82)(11)	(57-70)(5)	(57-82)(6)
	Yearlings	126[e]	-	126[e]
		(1)	(0)	(1)
	≥2 years	171.3± 27.1[f]	159.7±36.4[f]	177.2±22.9[f]
		(118-212(9)	(118-185)(3)	(150-212)(6)

1) Processed carcass weight = weight in kg of carcass bled, without viscera, skull, skin and lower legs.

2) Mean ± S.D. subtended in brackets by range and sample size.

abcdef) Same superscript indicates no significant difference.

ab) Refers to differences in weight between sexes.

cdef) Refers to differences in weight between area.

yearlings F = 0.41, p = 0.538; ≥2 years F = 0.134 , p = 0.7166), nor among islands for older animals (yearlings F=0.446, p=0.5209; 2 years F = 1.732, p = 0.193).

The percent mandible marrow fat in calves was greater on the island of Möja than on Utö and on Muskö (F = 3.62, p = 0.031). No differences in mandible marrow fat were seen among older animals. In ≥2-year-olds, females had a greater percent mandible marrow fat than males (females 76.0±8.8 %, range 41-84 %, n = 23; males 63.0±10.7 %, range 30-79, n = 20)(F = 18.9, p = 0.0001).

All calves shot on Utö in 89/90 were judged to be in poor condition. A decreasing trend was seen 90/91, 91/92, and 92/93 when 84%, 62%, and 50% respectively, were in poor condition (x^2 = 6.063, p = 0.19). In 93/94, when the sample consisted only of animals judged to be small (as in 89/90), 83%

Table 8. Indicators of size and condition of moose shot at Utö, Muskö, and Möja, 1989-94.

	Mandible length (mm)[1]	Mandible marrow fat (g/100 g)[1]
Utö		
Calves	294±18 (240-328)(73)[ab]	44±14 (13-64)(78)[d]
Yearlings	394±10 (382-410)(8)[c]	72± 6 (62-78)(9)[f]
≥2 years	424±14 (376-453)(26)[c]	71±10 (41-84)(32)[f]
Muskö		
Calves	281±19 (257-304)(7)[a]	38±15 (11-58)(7)[d]
Yearlings	400±26 (377-428)(3)[c]	64± 9 (54-72)(3)[f]
≥2 years	432±41 (381-493)(6)[c]	64 ±18 (30-79)(6)[f]
Möja		
Calves	308± 7 (303-318)(4)[b]	59± 8 (46-65)(5)[e]
Yearlings	(0)	(0)
≥2 years	447±16 (436-465)(3)[c]	68±10 (56-77)(5)[f]

1) Mean ± S.D. followed in brackets by range and sample size.

abc) Mean value superscripted with the same letter do not differ in mandible length between areas.

def) Mean value superscripted with the same letter do not differ in mandible marrow fat between areas.

were in poor condition.

Availability and Utilisation of Browse

Twenty-six transects with a total of 405 vegetation plots were surveyed on Utö. Approximately 50% of the study area was covered by forest, 30% by rock impediment, and 7% was classed as bog, marsh, and beach; the remainder was categorized as "other" (roads *etc.*). About 16% of the forest was <20 years of age and about 64% was 41 years or older. Woody browse species with the greatest cover included *Picea abies*, *Pinus sylvestris*, and *Betula pendula* (Table 9). The accumulated browsing was highest for *Sorbus aucuparia*, *Populus tremula*, and *Salix* spp. Winter browsing during 1992-1993 was most pronounced on *Juniperus communis*, *Populus tremula*, and *Pinus sylvestris*; *Picea abies* and *Betula pubescens* were the least browsed.

Population Density

The moose population was estimated at 1.4 moose/km^2, after corrections for moose shot during the 92/93 hunt. This was based on 152 pellet groups deposited over a winter period of 187 days on the survey area of 0.041 km^2.

DISCUSSION

Elaphostrongylus alces is well established on Utö where only moose are known to be infected. Like other *Elaphostrongylus* spp. (Mitskevich 1964, Panin 1964, Hale 1980, Skorping and Halvorsen 1980, Watson and Kean 1983, Demiaszkiewicz 1987), *E. alces* uses a diversity of terrestrial gastropods as intermediate hosts. Seven species were found naturally infected, with a mean of 4.3± 5.2 (1 - 20) larvae. All are herein reported for the first time as naturally infected intermediate hosts of *E. alces*.

Table 9. Moose browsing in 405 vegetation plots on Utö, April 1993.

Browse species	No. of plots with species	% cover in 405 plots	Accumulated browsing[1]	Previous winter's browsing[2]
Pinus sylvestris	176	3.56	1.3	7.2
Picea abies	164	7.05	0.02	0.0
Juniperus communis	59	0.74	1.7	11.4
Betula pubescens	61	0.98	1.6	2.4
Betula pendula	82	1.19	1.8	4.9
Sorbus aucuparia	53	0.27	2.0	3.6
Populus tremula	19	0.23	2.3	10.8
Salix spp.	32	0.22	2.0	3.6
Quercus robur	5	0.06	1.2	6.0

[1)] Mean value of codes (none=0, weak=1, moderate=2, and heavy=3) in the number of plots with the tree species.

[2)] Mean of class median values recorded for each plot with the tree species (none=0%, weak=5%, moderate=30%, heavy=75%).

Succinea spp., *Deroceras agreste* and *D. reticulatum* may be the most important in the transmission of *E. alces* at Utö , as they were often found high up on vegetation when the weather was damp. *Arion subfuscus*, found on ground vegetation, could be more important in the infection of grazing calves. *Limax cinereoniger* and *Zonitoides nitidus* were never found on vegetation but on or in ground litter and may, therefore, be less important in the transmission of *E. alces*. This may also be true for *Vitrina pellucida* which Skorping and Halvorsen (1980) considered to be a poor intermediate host for *E. rangiferi* because larval development in it was slow.

The prevalence of *E. alces* in moose calves on Utö was rather high (up to 67% with adult worms; 71% with adults and/or eggs/larvae in meninges; 64% with dorsal-spined larvae in feces). However, little comparable data exists for moose elsewhere. The prevalence of *E. alces* in moose on the adjacent mainland is unknown. In a study of 144 moose shot in Gävleborgs län (central Sweden) during the autumn hunting season of 1986 and 1987, 59% had nematode larvae in lung tissue and/or feces; adult *E. alces* were found in 31% of these animals (M. Stéen unpubl. data). Adult *E. alces* were recovered from epidural tissues, sciatic nerves, and muscle fasciae in 49% of 35 moose necropsied at the National Veterinary Institute, Uppsala, Sweden, in the first five months of 1985 (Stéen and Rehbinder 1986). Stuve (1986) found dorsal-spined larvae in the feces and/or lungs of 35% of moose in southern Norway; 31% of the calf cohort had these larvae.

Although the prevalence and intensity of *E. alces* infection did not differ statistically during the 3-year period in which all calves and yearlings were culled, a downward trend was evident. Fewer calves with heavy infections were found in year three. Also, more calves in year three had no inflammatory response in the meninges. Those that did had an acute rather than chronic reaction. This may indicate that moose calves were infected later in the season, i.e. in late summer/early autumn. Infection earlier in life may be characterized by more adult worms being detectable during the hunting season and by more chronic lesions around eggs and larvae. Our hypothesis that the transmission rate of *E. alces* can be altered by eliminating younger, more frequently infected animals cannot, therefore, be rejected. Furthermore, a more pronounced decline in infected calves after culling might have been delayed because of the longevity of first-stage larvae (Lorentsen and Halvorsen 1986) and the ability of infected gastropods to survive over-winter (Halvorsen and Skorping 1982).

We found no significant difference in the weights of infected and uninfected calves on Utö. Similarly, Stuve (1986) found no difference in the weights of calf and yearling moose with and without *Elaphostrongylus* in Norway. Stuve (1986) did, however, find that infected adult moose (≥2 year) were lighter than uninfected adults.

Mean processed carcass weights of moose calves harvested over the 5-year period on Utö (45.4±10.4 kg) and on Muskö (48.3±7.4 kg) were considerably lighter than those from two adjacent regions on the Swedish mainland in the autumn of 1989 (60±5.5, $\underline{n}$ = 41 and 67±16.0 kg, $\underline{n}$ = 123) ($p<0.001$) (R. Bergström unpubl. data). They were also lighter than calves harvested from 17 hunting regions throughout Sweden which ranged from 60 to 81 kg. Moose on Utö were also lighter than those examined by Stuve (1986) in southern Norway where calves on average were heavier by 20 kg , yearlings by 25 kg, and ≥2-year-olds by 40 kg ($p<0.001$). The calves on the island of Möja on the other hand, were similar in weight (65.6±8.2 kg) to the mainland calves. However, no differences were evident between Utö and Möja between the yearling and ≥2 years old category. More detailed studies of differences between conditions on Utö and Möja may help to explain why calves on the former were under weight. Ongoing research suggests that body weights of moose harvested in Sweden generally are declining somewhat, but not as much as seen in the calf cohort on Utö (R. Bergström, unpublished data).

Mandible lengths (294±18 mm, $\underline{n}$ = 73) were shorter than those of calves from regions in central Sweden (312±15.3 mm, $\underline{n}$ = 82 to 326±8.5 mm, $\underline{n}$ = 35; $p<0.001$) (H. Sand, Grimsö Wildl. Res. Stn, unpubl. data). Therefore, calves on Utö are not only lighter, but also smaller than those on the mainland.

The number of moose calves judged to be in poor condition decreased by at least 17% between 89/90, when only the smallest animals were shot, and 93/94, when the same collecting criteria were used. There was also a trend toward improved condition over the three intervening years when all calves and yearlings were collected. Data on mandible marrow fat, however, showed no consistent trend, possibly because of the large amount of annual variation in this parameter as reported by others (Cederlund *et al.* 1986, Ballard and Whitman 1987). Although the extreme low calf weights observed in the beginning of this study have not been recorded since 91/92 and a trend toward improved condition may be evident, further study is required to determine whether the culling of younger animals will increase the mean weights of moose calves born at Utö.

The moose population density at Utö was reduced from 2.0/km^2 in 1984 to 1.4 /km^2 in 1993. Several authors have described an inverse relationship between animal density and cervid body size. A study of roe deer by Klein and Strandgaard (1972) showed that roe deer body size was density dependent and determined by social pressures that affect energy expenditure and competition for food, especially during spring and early summer when food of high quality may have been limited. Saether and Heim (1993) found a correlation between herb biomass in the mother's summer home-range and calf weights. Nudgent and Frampton (1994) described a difference in size of fallow deer from areas with different availability of preferred foods. They also suggested that competition for food was a limiting factor until the population was reduced to about half the carrying capacity in the study area.

Lomolino (1985) reexamined "the island rule" and concluded that it accounts for a graded trend from gigantism in smaller species of insular mammals to dwarfism in larger species. Limited food supply was considered to be the main factor in reducing size of large artiodactylids living on islands. We have not studied herbs, but winter browse did not appear to be over utilized at Utö. Light browsing on preferred foods such as *Sorbus aucuparia* and *Salix* spp. during the previous winter, yet, relatively heavy accumulated browsing, may indicate that these species are mainly browsed during summer. Nontheless there were no clear indications that limited food is the cause of low weights and small body size at Utö. Weights of calves harvested in autumn are also known to be related to birth date. Schwartz *et al.* (1994) showed that calves from a second estrus breeding are lighter during their first summer and fall than calves conceived at first estrus. However, a confined high density population and a sex ratio of 51 bulls/100 cows observed in October, 1985 to 1988 on Utö probably ensures that most cows are bred in their first estrus (Timmermann 1992).

When discussing populations on islands, the question of inbreeding always arises. Ralls *et al.* (1979), reported effects of inbreeding in small ungulate populations and stated that inbred calves often succumbed to inanition and a variety of miscellaneous medical problems and infections not found in noninbred calves. Studies on the genetic diversity in moose from Utö are planned. The islands, however, are not totally isolated and moose have been seen swimming to and from the islands.

In conclusion; the moose population on Utö is relatively dense. Calves are smaller and have lower weights than calves on the mainland. The low weights cannot at present be related to infection with *E. alces*, and there is no indication that the low weights are related to lack of browse. Culling appeared to reduce the intensity of *E. alces* infection in the calf population. *Succinea* spp. are the most common intermediate host and, together with *Deroceras agreste*, *D. reticulatum*, and *Arion subfuscus*, are the most probable source of *E. alces* infection. Future moose management should include research designed to explain the differences between the moose populations at Utö and Möja. Further studies are also required to follow the effects of culling on *E. alces* as well as on the moose population at Utö.

ACKNOWLEDGEMENTS

We thank the hunters at Utö for their cooperation, as well as Å. Bäverlid, E. Carlman, B. Ekberg, M. Gustavsson, A. Karlsson, M. Källgren, A-C. Larsson, H. Mann, U. Nilsson, L. Olsson, O. Paulrud, S. Persson, B. Sundgren, B. Söderberg, S. Törnlöv, M. Vikberg, and G. Öhman for assistance in the laboratory and field. We are grateful to prof. A. Skorping and his staff at Tromsö University for their excellent teaching assistance in finding elaphostrongylines in gastropods, and we thank Dr J. Bengtsson for advice on gastropod species identification.

This manuscript has benefitted greatly by suggestions from Alces editor Dr. M. Lankester, as well as comments from two anonymous reviewers.

The study was supported by Michael Forsgrens Stiftelse, Skärgårdsstiftelsen, Stockholms länsstyrelse viltskadefond, Swedish Hunters' Association, Reg. vet. och Fru Carl Ahlgrens stipendiefond, Gustaf Lindströms minnesfond, and Fredrika-Bremer-Förbundet.

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