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ORIGINAL PAPER

The effects of an abundant ectoparasite, the deer ked (*Lipoptena cervi*), on the health of moose (*Alces alces*) in Finland

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Abstract The deer ked (*Lipoptena cervi*, Diptera, Hippoboscidae) is a haematophagous parasitic fly of the moose (*Alces alces*) and other cervids, and it is very common in southern and central parts of Finland. The aim of this study was to determine how the intensive parasitism caused by the deer ked affects the health and welfare of the moose. Moose blood samples (n=78) were collected from deer ked-infested and ked-free regions at 62–68° N and analysed for haematology and clinical chemistry. In addition, tissue samples of moose (n=23) were collected from a deer ked-infested region at 62° N to determine how the parasite load correlates to several physiological variables of the host. The differences in the blood and plasma values between the deer ked-free and ked-infested animals were minor. In the infested regions, the moose had higher mean corpuscular haemoglobin concentrations unlikely to have been caused by the parasitism. The intensities of deer keds had no consistent correlations with the values of plasma clinical chemistry, endocrinology, amino acids, tissue enzyme activities or body energy stores. However, the hepatic percentages of several individual n-3 polyunsaturated fatty acids (PUFA) and the n-3 PUFA sum correlated inversely with the intensity and density of deer keds. Although a wide array of physiological variables was determined, only minor effects caused by the heavy deer ked parasitism could be detected, suggesting that the moose might tolerate this parasite relatively well.

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Introduction

The deer ked (*Lipoptena cervi*, L., Diptera, Hippoboscidae) is a haematophagous ectoparasite of cervids that has been present in Finland since the early 1960s (Hackman et al. 1983) with its current northern distribution limit at approximately 65° N (Välimäki et al. 2010). The deer ked can parasitise several cervids, such as the red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*; Kadulski 1996; Szczurek and Kadulski 2004), wild forest reindeer (*Rangifer tarandus fennicus*) and semi-domesticated reindeer (*Rangifer tarandus tarandus*; Kaunisto et al. 2009), and it has been observed also on particular domestic animals, for instance, the cattle (*Bos taurus*) and sheep (*Ovis aries*; Mehlhorn et al. 2010). In Finland, the principal host is the moose (*Alces alces*; Välimäki et al. 2011) with 1,700–10,600 keds per animal in the eastern part of the country depending on the sex and age of the host (Paakkonen et al. 2010). The deer ked is viviparous (Meier et al. 1999) and has one generation per year (Ivanov 1981). The imago survives for 120–180 days on its host, and during this period, female keds can produce 20–32 pupae, which fall on the forest floor. The new generation emerges in August–early November (Popov 1965; Ivanov 1981).

Blood-feeding ectoparasites may cause deleterious health effects on their hosts, e.g. anaemia, decreased haemoglobin concentrations or red blood cell counts. Findings of this type were observed in ruminants parasitised by arthropods (Stacey et al. 1978; Williams et al. 1978; Stromberg et al. 1986; O'Brien et al. 1995; Pérez et al. 1999), and also increased neutrophil, eosinophil and total leukocyte counts were documented (Losson et al. 1988; O'Brien et al. 1995). Ectoparasites may also have indirect effects on their hosts causing, e.g. decreased weight gain (Williams et al. 1977; Harvey and Launchbaugh 1982) or weight loss (Corrier et al. 1979). Furthermore, the feeding patterns of haematophagous ectoparasites make them medical and veterinary concerns, and the deer ked has been proposed to act as a vector for bacteria of the genera *Borrelia* (Doby et al. 1994) and *Bartonella* (Dehio et al. 2004) and for *Megatrypanum* protozoa (Böse and Petersen 1991). Information on the health risks of the deer ked on its hosts is scarce. However, the effects of this parasite on the well-being of captive reindeer were documented to be minor, although the intensity of parasitism ($n \leq 300$ keds/reindeer) was clearly lower than on wild moose in eastern Finland (Paakkonen et al. 2010, 2011). Madslien et al. (2011) reported recently that the deer ked could have induced alopecia, dermatitis and inflammatory skin reactions to Norwegian moose further emphasising the need to examine in detail the heavily parasitised Finnish moose population.

The present study was undertaken to determine how the intensive deer ked parasitism affects the health and well-being of wild moose. The specific aims were to investigate (1) if selected haematological and clinical chemistry variables of the moose differ between deer ked-infested and deer ked-free regions in Finland and (2) how the intensity of deer ked parasitism or (3) the sex and maturity of the host affect these variables. As ectoparasites have previously induced several physiological responses in ruminants, it can be hypothesised that deer ked parasitism would have deleterious effects on the physiology of the moose.

Material and methods

The tissue samples of moose were collected from the deer ked-infested region of Liperi commune, eastern Finland (62°31′ N, 29°08′ E; group I; $n=23$) between October 7 and November 26, 2006 during the legal hunting season. Group I consisted of eight bulls, eight cows (three gestating) and seven calves (six males and one female). The average intensities of deer ked parasitism on these moose were reported previously and they were 10,616±1,375 keds on the bulls, 3,549±587 on the cows and 1,730±191 on the calves, while the average densities were 35.7±4.4, 11.8±1.7 and 9.4±1.1 keds per skin dm^2, respectively (Paakkonen et al. 2010). Most of the keds (95±1 %) were blood-fed at the time of sampling and the blood-fed males were heavier than the blood-fed females (20.5±0.2 vs. 15.4±0.1 mg), while the weights of the non-blood-fed deer keds did not differ by sex (4.1±0.3 vs. 4.0±0.3 mg). The duration of chase was determined as the time interval from the first contact by hunters or dogs until the killing of the moose. The age was estimated based on the annual rings of incisors (modified from Rolandsen et al. 2008). The average ages of the bulls and cows were 3.1±0.4 and 4.4±0.6 years; the moose less than 1 year of age were classified as calves.

The livers were dissected and tissue samples taken from *musculus rectus abdominis* as well as from gluteal subcutaneous (SC) and intraabdominal (retroperitoneal, RP) adipose tissues. The samples were frozen and stored at −80°C. The weights of the carcass, pelt, liver, kidneys and omentum together with the lengths of the carcass and pelt were measured. An estimate of the body mass (BM) was calculated from the weight of the carcass (Wallin et al. 1996). The thickness of SC fat reflecting the nutritional state (Stephenson et al. 1998) was measured from an incision in the gluteo-sacral region (Finnish Game and Fisheries Research Institute 2012). The tissue glycogen, protein and lipid concentrations and enzyme activities were analysed as outlined in Mustonen et al. (2006b), and the plasma amino acid (AA) levels were determined with ion-exchange chromatography (Biochrom 30 Amino Acid Analyzer, Biochrom Ltd, Cambridge, UK). For the fatty acid (FA) analyses of total lipids, samples of adipose tissues, muscle, liver and plasma were transmethylated

according to Christie (1993). The formed FA methyl esters were extracted with hexane and analysed by a gas–liquid chromatograph (6890 N network GC system with a flame ionisation detector and 5973 mass selective detector, Agilent Technologies, Santa Clara, CA, USA) as described by Paakkonen et al. (2011).

To assess the possible effects of deer ked infection on moose haematology and clinical chemistry, a larger material of whole blood and EDTA-plasma samples was collected to supplement group I (n=20 for blood samples of high quality) in other deer ked-infested regions in western and central Finland (group II; n=34; 63°40′–65°47′ N, 24°31′–25°57′ E) and in deer ked-free regions in northern Finland (group III; n=24; 65°01′–68°54′ N, 24°43′–27°01′ E) between October 1 and December 12, 2006 by local hunters (Fig. 1). Group II consisted of 7 bulls, 12 cows and 15 calves (4 males and 11 females) and group III of 8 bulls, 11 cows and 5 calves (3 males and 2 females). The complete blood count was analysed with the Vet abc Animal Blood Counter (ABX Hematologie, Montpellier, France) using the equine calibration at the Municipal Veterinary Clinic of Joensuu within 48 h of sampling. The results were mostly comparable to previous data on moose haematological values (Adolfsson 1993). The plasma clinical chemistry variables were determined with reagents of Randox Laboratories Ltd (Crumlin, UK) as described by Mustonen et al. (2006a, b, 2009) and Paakkonen et al. (2011). All these analyses were performed with the Technicon RA-XT^{TM} analyser (Technicon Ltd, Swords, Ireland). The plasma leptin, ghrelin, insulin and cortisol concentrations were determined with commercial radioimmunoassay kits (Mustonen et al. 2005, 2009; Paakkonen et al. 2011). The hormone assays were validated by way of serial dilutions of the moose plasma resulting in linear changes in B/B_0 values (B = sample or standard binding, B_0 = maximum binding) parallel with the standard curves produced with the standards of the manufacturers (Supplement 1).

Comparisons between the study groups and between the age and sex categories within group I were performed by the one-way analysis of variance (ANOVA) and the Duncan's post hoc test with the SPSS program (v17.0, SPSS Inc, Chicago, IL, USA). For nonparametric data, the Kruskal–Wallis ANOVA followed by the Dunn's post hoc test was performed with the SigmaPlot program (v11.0, Systat Software Inc, Chicago). Comparisons between two groups were performed with the Student's t test for parametric data and with the Mann–Whitney U test for nonparametric data using the SPSS program. In group I, correlations of the deer ked numbers and densities (data from Paakkonen et al. 2010) with the measured health-indicating variables (present report) were calculated with the Spearman correlation coefficient (r_s). In all the univariate statistical tests, a p value < 0.05 was considered statistically significant. The results

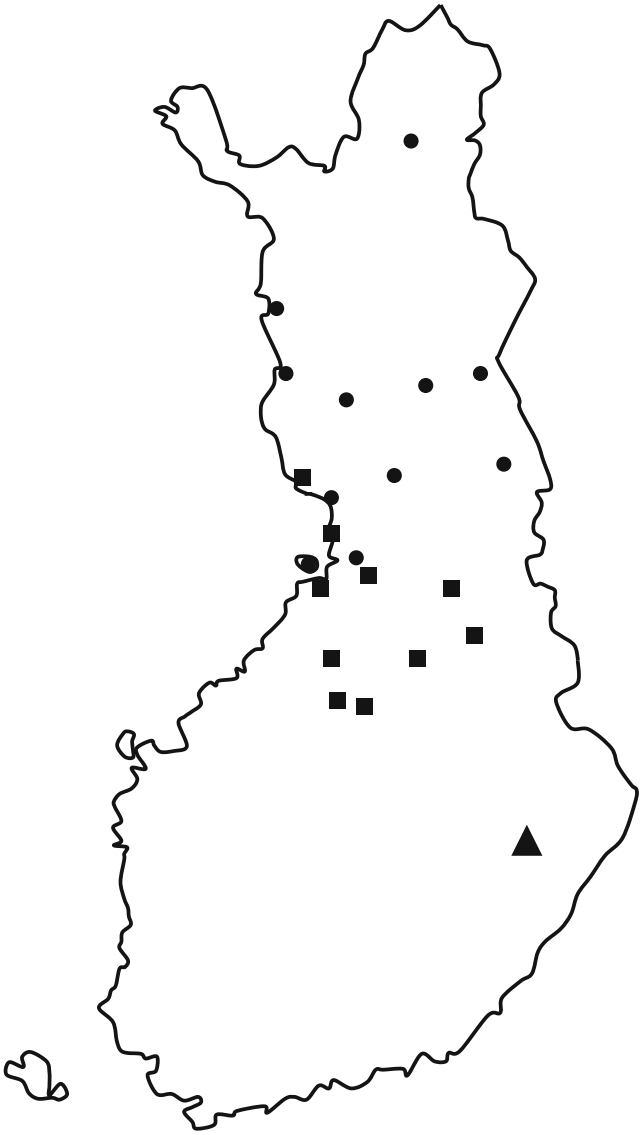

Fig. 1 The map of Finland depicting the locations, where the blood samples of the moose (n=78) were collected from deer ked-infested (*filled triangle*, group I; *filled square*, group II) and deer ked-free regions (*filled circle*, group III) between October 1 and December 12, 2006

are presented as the mean±SE. To analyse the relationships in the FA composition according to the different groups and tissues, the data were subjected to the multivariate principal component analysis (PCA) with the SIRIUS v6.5 software package (Pattern Recognition Systems AS, Bergen, Norway; Kvalheim and Karstang 1987).

Results

Moose group I had the highest mean corpuscular haemoglobin (MCH) and groups I and II both had significantly higher mean corpuscular haemoglobin concentrations (MCHC)

than the northern group III (Table 1). The leukocyte counts and relative amounts did not differ between the groups. The cholesterol levels in plasma and the lipoprotein fractions thereof were the lowest in group I (Table 2). Groups II and III had higher ammonia and uric acid concentrations and lower alanine aminotransferase activities than group I. Group I had lower creatinine concentrations than group III and higher urea/creatinine ratios than group II. The duration of chase correlated positively with the plasma creatine kinase (CK) activities in group I (r_s=0.520, p<0.05).

The adult moose of group I had higher haemoglobin and MCH values than the juveniles, and the cows had higher mean corpuscular volumes (MCV) than the bulls and calves (Supplement 2). The juveniles displayed also lower plasma creatinine concentrations than the other moose (Supplement 3). As expected, the adult moose had higher estimated BM and masses of kidneys and pelts as well as longer carcasses and pelts than the calves, and the bulls had also higher masses of testicles than the male calves (Supplement 4). The cows had heavier livers, omental and RP fat masses and thicker SC fat layers than the bulls and calves. The liver glucose-6-phosphatase activities were higher in the bulls than in the cows and calves while the cows had lower RP fat lipase activities than the other groups (Supplement 5). The adults displayed higher plasma 1- and 3-methylhistidine concentrations than the calves with no differences in the other AA (Supplement 6).

The total numbers and densities of deer keds correlated positively with several morphological variables of the hosts (BM and masses of kidneys, testicles and pelts and length of pelts, r_s=0.414–0.718, p<0.05), and the intensity of parasitism correlated with the liver glucose-6-phosphatase activities (r_s=0.458–0.494, p<0.05). The intensity and density of deer keds correlated positively with the plasma lysine and threonine concentrations (r_s=0.479–0.560, p<0.05) and negatively with the alanine levels (r_s=−0.447 to −0.459, p<0.05).

According to PCA, the FA profiles of the tissues diverged from each other and the FA mostly responsible for these differences were 18:1n-9, 18:2n-6, 18:0 and 16:0 (Supplement 7). In addition, the hepatic FA composition, especially 18:1n-9, varied by the age of the moose (adults vs. calves). PCA also indicated that the FA composition of SC and RP fats as well as muscle differed by sex and age (bulls vs. cows vs. calves), and the FA explaining the largest part of this variation were 18:1n-9, 18:0 and 16:0.

In general, the adipose tissues studied contained more 16:0, 18:0 and saturated FA (SFA) as a total than liver, muscle or plasma (Table 3). In addition, the proportions of total monounsaturated FA (MUFA) were the highest in SC fat and the lowest in plasma. The percentages of 16:1n-7 were the highest in liver and the lowest in muscle. Plasma and liver, however, contained less 18:1n-9 than the other tissues and the highest proportions of 18:1n-7 were observed in RP fat. The n-3 and n-6 polyunsaturated FA (PUFA) totals were the lowest in adipose tissues. The same trend was also observed for several individual n-3 PUFA. Also, the unsaturated FA (UFA)/SFA ratios were the lowest in adipose tissues. The proportions of *trans* FA were the highest in liver and the lowest in muscle.

The SC fat of the bulls contained lower percentages of 16:0 and higher percentages of 18:0 than those of the cows

Table 1 The effects of deer ked parasitism on the haematological variables of the moose (mean±SE)

	Group I (n=20)	Group II (n=34)	Group III (n=24)
Red blood cells (10^6/mm^3)	5.54±0.25	5.43±0.21	5.40±0.22
Haemoglobin (g/L)	130±6	118±4	118±5
Haematocrit (%)	36.5±1.8	33.7±1.3	35.1±1.6
Mean corpuscular volume (μm^3)	65.2±1.0	62.5±0.7	65.0±1.1
Mean corpuscular haemoglobin (pg)	23.5±0.3 b	22.1±0.3 a	21.9±0.4 a
Mean corpuscular haemoglobin concentration (g/dL)	36.1±0.3 b	35.3±0.2 b	33.8±0.8 a
Red blood cell distribution width (%)	16.0±0.2	15.6±0.2	15.4±0.2
Platelets (10^3/mm^3)	117±35	78±13	106±21
Mean platelet volume (μm^3)	5.5±0.2	5.4±0.1	5.3±0.1
White blood cells (10^3/mm^3)	2.76±0.30	2.26±0.19	2.45±0.19
Lymphocytes (10^3/mm^3)	0.5±0.1	0.5±0.1	0.6±0.1
Monocytes (10^3/mm^3)	0.1±<0.1	0.1±<0.1	0.1±<0.1
Granulocytes (10^3/mm^3)	2.2±0.3	1.7±0.2	1.8±0.2
Lymphocytes (%)	21.6±1.9	25.3±2.6	30.9±5.2
Monocytes (%)	5.5±0.6	5.1±0.3	4.9±0.4
Granulocytes (%)	72.9±2.3	69.6±2.7	68.8±3.2
Eosinophils (%)	17.3±2.1	16.3±1.4	17.8±1.8

Means with no common letters differ at p<0.05 (one-way ANOVA)

Table 2 The effects of deer ked parasitism on the plasma clinical chemistry of the moose (mean±SE)

	Group I (n=20)	Group II (n=34)	Group III (n=24)
Glucose (mmol/L)	8.15±0.81	6.89±0.39	7.11±0.94
Total cholesterol (mmol/L)	1.05±0.07 a	1.52±0.06 b	1.38±0.08 b
Low-density lipoprotein cholesterol (mmol/L)	0.23±0.01 a	0.33±0.02 b	0.31±0.02 b
High-density lipoprotein cholesterol (mmol/L)	0.66±0.06 a	0.94±0.05 b	0.77±0.06 ab
Triacylglycerols (mmol/L)	0.63±0.11	0.87±0.11	0.75±0.09
Ammonia (μmol/L)	173±15 a	324±39 b	331±49 b
Urea (mmol/L)	4.00±0.36	2.71±0.36	3.61±0.54
Uric acid (μmol/L)	29.04±4.32 a	75.24±17.81 b	51.19±4.23 b
Creatinine (μmol/L)	185±12 a	210±11 ab	240±13 b
Urea/creatinine ratio	24.16±3.00 b	13.67±2.14 a	17.87±3.19 ab
Creatine kinase (U/L)	5,753±1,017	3,735±746	5,321±1,298
Alanine aminotransferase (U/L)	58.6±9.7 b	37.6±2.9 a	41.8±5.5 a
Aspartate aminotransferase (U/L)	148.3±25.2	103.1±13.1	137.9±19.2

Means with no common letters differ at $p<0.05$ (one-way ANOVA, Kruskal–Wallis ANOVA)

and calves, while the cows had higher MUFA sums, 18:1n-9 proportions and UFA/SFA ratios than the bulls and calves and lower PUFA sums than the calves (Supplements 8 and 9a). In RP fat, the percentages of 16:0 increased according to the sequence: bulls < cows < calves, while the proportions of 18:0 increased in the opposite order (Supplements 8 and 9b). The bulls had lower hepatic n-3 PUFA proportions (Fig. 2, Supplements 8 and 9c) and the same trend was also observed in other tissues (Supplement 8). The hepatic n-3/n-6 PUFA ratio of the gestating cows was lower than that of the non-gestating cows (0.84±0.03 vs. 1.18±0.12, Mann–Whitney U test, $p<0.05$). The calves had lower hepatic 18:1n-9 proportions than the adults (Supplements 8 and 9c). The age and sex of the moose had relatively minor effects on the muscle and plasma FA profiles (Supplements 8 and 9d–e). The proportions of several individual n-3 PUFA and the n-3 PUFA sum in liver and the percentages of 18:3n-3 in SC fat correlated negatively with the intensity and density of deer keds (r_s= −0.438 to −0.612, $p<0.05$), as did also the 16:0 proportions in liver and fat tissues (r_s=−0.517 to −0.603, $p<0.05$). The percentages of 18:0 in adipose tissues correlated positively with the intensity and density of parasites (r_s=0.499–0.574, $p<0.05$).

Table 3 The proportions (mol%) of selected fatty acids in different tissues of the moose of group I (mean±SE)

	Liver	Muscle	SC fat	RP fat	Plasma
16:0	12.12±0.38 a	16.19±0.85 b	17.14±1.05 bc	21.46±0.75 c	14.74±0.42 ab
18:0	26.58±0.52 bc	18.92±0.78 a	28.51±1.29 cd	34.40±1.01 d	23.17±0.66 ab
Σ:SFA	45.39±0.73 a	39.92±1.31 a	53.91±1.26 b	64.54±0.52 c	45.64±0.73 a
16:1n-7	1.15±0.05 b	0.75±0.07 a	0.99±0.11 ab	0.84±0.06 a	0.99±0.08 ab
18:1n-9	17.55±0.79 a	25.35±1.81 b	30.38±2.06 b	22.93±0.67 b	15.93±0.58 a
18:1n-7	2.58±0.11 b	1.92±0.07 a	2.25±0.20 ab	2.79±0.24 b	1.70±0.12 a
Σ:MUFA	25.27±0.98 ab	30.70±1.75 bc	37.16±1.85 c	29.07±0.46 bc	22.02±0.62 a
18:3n-3	2.67±0.15 bc	3.38±0.28 cd	1.50±0.15 a	1.99±0.13 ab	4.11±0.26 d
20:5n-3	2.33±0.19 c	1.21±0.18 bc	0.16±0.05 a	0.03±<0.01 a	1.44±0.11 c
22:5n-3	5.15±0.38 d	1.24±0.16 bc	0.34±0.12 a	0.06±0.01 a	2.03±0.12 cd
22:6n-3	2.38±0.18 d	0.18±0.03 b	0.09±0.03 ab	0.01±<0.01 a	0.87±0.07 cd
Σ:n-3 PUFA	12.88±0.80 c	6.27±0.63 b	2.33±0.25 a	2.14±0.13 a	8.70±0.47 bc
18:2n-6	7.00±0.25 bc	10.23±1.06 cd	1.98±0.16 a	2.15±0.10 a	17.17±0.55 d
20:4n-6	5.61±0.27 c	3.04±0.40 b	0.41±0.18 a	0.09±0.02 a	3.00±0.11 b
Σ:n-6 PUFA	13.25±0.51 b	13.60±1.46 bc	2.49±0.30 a	2.27±0.11 a	20.55±0.62 c
n-3/n-6 PUFA ratio	0.98±0.06 b	0.48±0.03 a	1.05±0.13 b	0.96±0.06 b	0.43±0.03 a
Σ:PUFA	27.04±1.00 bc	20.29±2.04 b	5.82±0.53 a	5.12±0.21 a	30.30±0.73 c
Σ:*trans* FA	1.37±0.09 c	0.52±0.04 a	1.11±0.05 bc	1.21±0.06 bc	1.02±0.07 b
UFA/SFA ratio	1.16±0.03 b	1.32±0.07 b	0.81±0.05 a	0.53±0.01 a	1.16±0.03 b

Means with no common letters differ at $p<0.05$ (Kruskal–Wallis ANOVA)

SC subcutaneous, *RP* retroperitoneal, *SFA* saturated fatty acid, *MUFA* monounsaturated fatty acid, *PUFA* polyunsaturated fatty acid, *FA* fatty acid, *UFA* unsaturated fatty acid

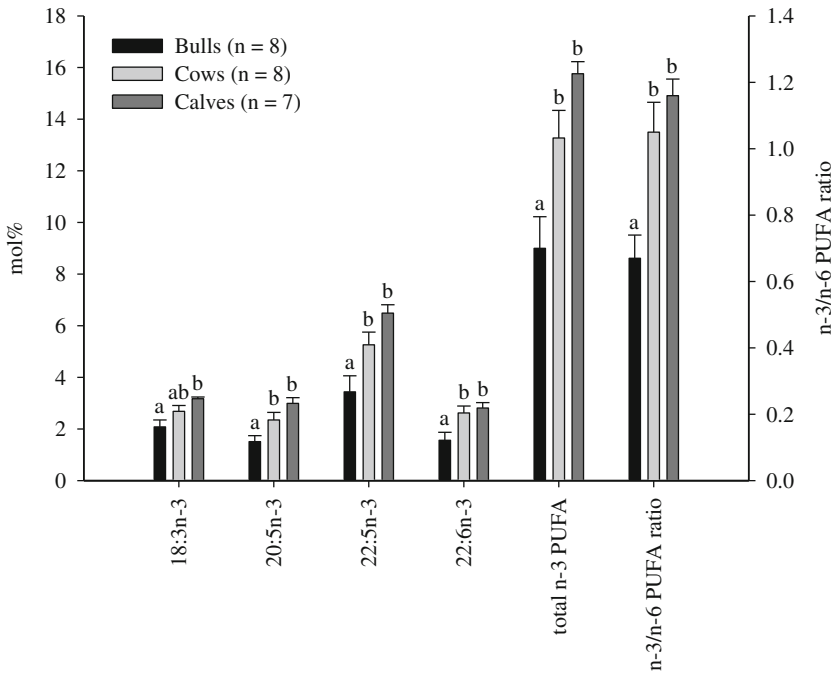

Fig. 2 The proportions (mole%) of selected n-3 polyunsaturated fatty acids (PUFA), total n-3 PUFA and n-3/n-6 PUFA ratios in the liver total lipids of the moose of group I (mean+SE). Means with no common letters differ at $p<0.05$ (Kruskal–Wallis ANOVA)

Discussion

The moose is parasitised by several eumetazoans, of which platyhelminths and nematodes are principally endoparasites, while most arthropods are ectoparasites (reviewed in Samuel et al. 2001). For example, *Paramphistomum cervi* is a rumen trematode commonly observed in North American moose (Hoeve et al. 1988), while *Dictyocaulus capreolus* is a nematode lungworm of the moose and other cervids (Gibbons and Höglund 2002). *Elaphostrongylus* spp. parasitise the nervous system of wild cervids, and for instance, *E. alces* was documented to infect Swedish moose (Stéen et al. 1997). The larvae of the moose throat bot (*Cephenemyia ulrichii*) mature in the pharyngeal cavity of moose (Nilssen et al. 2008; Angulo-Valadez et al. 2010). The moose may also serve as an intermediary host for endoparasites, such as the cestode *Echinococcus granulosus* (McNeill and Rau 1987). The winter tick (*Dermacentor albipictus*) is a common arthropod ectoparasite in North America with the documented intensity of over 30,000 ticks per moose (Samuel and Welch 1991). Many haematophagous insects of the order Diptera visit their hosts only briefly to consume blood. Dipterans that utilise the moose include various mosquitoes (Culicidae), black flies (Simuliidae), biting midges (Ceratopogonidae) and tabanids (Tabanidae; Samuel et al. 2001). Previous reports on the numbers of parasites on moose are scarce. In addition to data on winter ticks (Samuel and Welch 1991) and our previous study on deer keds (Paakkonen et al. 2010), Madslien et al. (2011) documented recently in Norway deer ked intensities of a similar magnitude (up to 16,500 parasites per host) to those on Finnish moose.

Due to the heavy parasitism of deer keds on moose (Paakkonen et al. 2010), it was hypothesised that the deer ked could have negative effects on the physiology and health indices of its host, but according to the present results, the influence was difficult to detect. Groups I and II had higher MCHC than group III but this was probably of a minor physiological significance and unlikely to have been caused by the parasitism. Anaemia or decreased red blood cell values have previously been documented due to haematophagous parasites at high intensities (for review, see Paakkonen et al. 2011). According to Ivanov (1981), deer keds consumed blood 15–20 times per day. Recently attached keds ingested 2–3 mg of blood at a time, and after their abdomen had distended, 4–5 mg. Thus, one deer ked could have consumed 30–100 mg of blood each day. Hypothetically, a moose bull with an estimated number of 10,000 keds (Paakkonen et al. 2010) would lose approximately 320–1,050 g blood every day, approximately 0.10–0.34 % of its BM. A cow would lose 105–355 g (0.03–0.10 % BM) and a calf 50–175 g (0.03–0.10 % BM). Based on the assumed blood volume of 8 % BM (Leighton 2000) and the average haematocrit value of group I, the estimated red blood cell mass of the bulls would be approximately 9 kg. Thus, the bulls would have to replace their total red blood cell population every 25–80 days, 1.8–5.6 times faster than normal as the estimated life time of red blood cells would be approximately 140 days in animals with a similar body size and maximal life span (Röhme 1981). Blood loss at this level would probably induce anaemia, but the results did not indicate any signs of that, similar to three deer ked-parasitised Norwegian moose with normal haemoglobin values (Madslien et al. 2011).

Severe blood loss would increase the degree of anisocytosis of erythrocytes and, subsequently, the red blood cell distribution width value (Davidsohn and Nelson 1974; Weksler and Moore 1990). Eventually, microcytosis (decreased MCV) and lowered MCH and MCHC would ensue. However, no signs of these effects were present, and based on these data, the blood consumption rate and the volume consumed by the wild deer ked may be lower than those documented in previous laboratory experiments (Ivanov 1981). Generally, the findings of the current study were quite similar to other experiments showing no statistically significant or physiologically relevant effects of ectoparasitism on haematological values (Williams et al. 1977; Schwinghammer et al. 1986a, b, 1987). The equally high percentages of eosinophils in the moose from all three regions including the deer ked-free area suggest that all these moose could have had high intensities of various eukaryotic parasites. This could complicate any attempts to distinguish the effects of a single parasite species.

Except of n-3 PUFA, the intensity of deer ked parasitism showed no consistent correlations with the tissue FA profiles of the moose but the age and sex affected some FA sums and/or indices. Muturi et al. (2005) documented that an increase in the n-3/n-6 PUFA ratio in gut mucosa could enhance host resistance against eukaryotic endoparasites. Especially important FA regarding immunity against parasitism could be 20:4n-6, 20:5n-3 and 22:6n-3 (Kumaratilake et al. 1997; Arun Kumar and Das 1999). In the present study, the highest deer ked intensities and densities were observed on the bulls (Paakkonen et al. 2010), and they also had the lowest hepatic 18:3n-3, 20:5n-3 and 22:6n-3 proportions and n-3/n-6 PUFA ratios in liver and muscle. The lower n-3 PUFA proportions and sums may be a sign of negative energy balance, as the mobilisation of n-3 PUFA is more efficient than that of n-6 PUFA during calorie restriction (Rouvinen-Watt et al. 2010). Finnish moose bulls were documented to be more active in autumn than cows (Heikkinen 2000), and this could reduce the time they allocate to feeding, especially during the mating season (Valste 2001), and be an explanation to this observation.

Generally, the calves had the highest n-3 PUFA proportions but the lowest parasite numbers and densities, and this might be a reason why the values of deer ked intensity and density correlated inversely with several hepatic n-3 PUFA. It remains to be determined if this observation on higher n-3 PUFA proportions and lower parasite numbers represents any causal relationship. Also, gestation reduced the hepatic n-3/n-6 PUFA ratio. This has some similarities to previous observations on humans, in which the plasma FA profiles showed reduced proportions of both n-6 and n-3 PUFA, but the decreases were more drastic in the n-3 pool (Holman et al. 1991). The moose in the present study had higher tissue n-3 PUFA proportions and sums than documented previously in captive reindeer (Paakkonen et al. 2011). This may be due to different n-3 PUFA proportions in the natural diet of moose compared to the commercial feed of captive reindeer (Chernobrovkina et al. 2008; Vedernikov and Roshchin 2010; Paakkonen et al. 2011).

The lack of consistent correlations between the intensity and density of parasitism and the tissue glycogen or protein concentrations, enzyme activities, plasma clinical chemistry, endocrinology and AA values gives further evidence that, although intense, the parasitism did not induce detectable physiological changes on the moose. Variables of potential interest in this respect would be stress-related hormones and parameters indicating increased catabolism and, thus, potential risk of undernutrition due to parasite load or harassment. Increased plasma cortisol concentrations have previously manifested stress in parasitised cattle (Schwinghammer et al. 1986a, b, 1987), but no correlation with the intensity of parasitism could be observed in the moose, similar to captive deer ked-infected reindeer (Paakkonen et al. 2011). The potential hazards of harassment and skin irritation include increased duration of time allocated to energy-consuming activities (Schwinghammer et al. 1986a, b, 1987; Mörschel and Klein 1997; Hagemoen and Reimers 2002) causing, e.g. reduced weight gain of the host (Williams et al. 1977). This could have been reflected in the variables of nitrogen (urea, ammonia, AA) and fat metabolism (lipid stores, lipase activities, plasma lipids), or in the values of weight-regulatory hormones (leptin, ghrelin, insulin). These values did not correlate with the intensity or density of parasites—not unlike in captive reindeer after an experimental deer ked infection (Paakkonen et al. 2011).

Intensive muscle work, such as running, is often reflected as elevated plasma CK activities (Adlercreutz et al. 1983), and harassment by deer keds could hypothetically increase physical activity levels of moose and hence their CK levels. Again, the results of this study did not support this, as only the duration of chase correlated with the plasma CK activities. After summertime food abundance, moose are generally in a good physical condition in autumn (Timmermann and McNicol 1988), which may reduce the possible negative effects of deer keds, as the nutritional state of the host can affect its response to parasitism (Nelson 1984). As the data of this experiment were collected during a short autumnal period, additional studies in winter and spring will be required to confirm the present results. However, sampling in other seasons is logistically difficult, as moose hunting in Finland is subject to licence and allowed only in autumn. Still, it would be interesting to assess the impact of the continuing presence of parasites (but at a possibly decreasing intensity) on the health of moose in winter and early spring. The negative energy balance during this period (Timmermann and McNicol 1988) could unmask the possible physiological effects of parasitism.

North American moose displayed alopecia when parasitised by the winter tick (Glines and Samuel 1989; Mooring and Samuel 1999), and deer ked parasitism was suggested to be a causative factor for the hair loss observed in Norwegian moose as well (Madslien et al. 2011). With the exception of one individual with minor hair loss of unknown aetiology, the majority of the moose in the present study showed no signs of this (Paakkonen et al. 2010). Deer keds could possibly cause less irritation than winter ticks or the intensity of deer ked parasitism on Finnish moose—despite the high parasite numbers counted—could be too low to increase grooming activity enough to promote hair loss, but more studies in winter and spring are needed to verify this. Thus, it seems that the moose in the study area tolerate deer ked parasitism relatively well. While the deer ked is a recent newcomer in Finland (Hackman et al. 1983), there are reports of high deer ked intensities on moose in the former Soviet Union (Popov 1965; Ivanov 1981). The Finnish moose population was hunted near extinction by the 1920s and partly replenished by the Soviet stock after World War I (Nygren 2009)—presumably together with its parasites. It could be surmised that the co-existence of the moose and the deer ked has endured for long periods of time and allowed the moose to adapt to this parasite.

Conclusions

1. The haematological and clinical chemistry variables of the moose did not show significant variation between the studied deer ked-infested and deer ked-free regions in Finland.
2. The intensity of deer ked parasitism did not correlate consistently with the measured physiological variables. However, the proportions of several hepatic n-3 PUFA correlated negatively with the parasite intensity and density, but it remains to be determined if this represents a causal relationship.
3. The bulls had lower n-3 PUFA proportions in their tissues than the cows and calves. Apart from slightly different haematological and FA profiles, the bulls, cows and calves were fairly similar in their physiological variables.

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Ethical standards The authors declare that all procedures included in this article comply with the current laws of Finland.

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