BLOOD CHEMISTRY AND ENDOPARASITES OF THE MOUNTAIN HARE (LEPUS TIMIDUS L.) IN HIGH AND LOW DENSITY POPULATIONS

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ABSTRACT: In order to study the effect of high population density on the condition, blood characteristics and helminth parasitism of mountain hares (*Lepus timidus*), 12 specimens were shot in December 1982 and 12 more in February 1983 on the west coast of central Finland (group 1, dense population). In addition 14 hares were shot in December 1982 about 100 km from group 1 (group 2, dense population). Group 3 consists of 15 hares from stable, rather low density populations shot in southern Finland during three previous winters. The hares in group 1 were the lightest, had the least fat and were the most seriously infected with *Protostrongylus pulmonalis* and *Trichostrongylus retortaeformis*, while those in group 2 were the heaviest and had the highest Ca, Mg, alkaline phosphatase and creatinine values. The group 3 hares had the most fat. The group 1 animals shot in February 1983 had higher Ca, Mg, triglyceride and cholesterol values than those shot in December 1982. It seems that high population density combined with a lack of suitable food leads to poor condition and high endoparasite abundances. The differences in Ca and Mg are probably due to diet. The higher creatinine values in group 2 and in the hares with little or no *T. retortaeformis* infection may be due to the greater muscle mass.

Key words: Mountain hare, *Lepus timidus*, endoparasites, condition, blood chemistry, population density.

INTRODUCTION

Blood characteristics (Rosen and Bischoff, 1952; Franzmann and LeResche, 1978; Nieminen, 1980; Kie et al., 1983) and fat levels (Rausch, 1950; Anderson et al., 1972; Franzmann et al., 1978; Soveri and Aarnio, 1983; Soveri et al., 1988) have been widely used to evaluate the condition of mammals, and the presence of a large number of parasites also may indicate poor condition of the host individuals (Yuill, 1964; Jacobson et al., 1978). Populations of the mountain hare fluctuate markedly in Finland, but not in an obviously cyclic manner (Jokinen and Häkkinen, 1982). The role of parasites in population fluctuations in mammals is unclear. Keith et al. (1985, 1986) studied the endoparasites of snowshoe hares in North America and Haukisalmi et al. (1988) and Haukisalmi and Henttonen (1990) the intestinal parasites of voles in northern Finland during different phases of the population cycle, and their results suggest that helminths do not have any clear effect on population cycles. Research has been conducted in Europe into the

blood chemistry of the European hare (Mihardja et al., 1979; Tataruch and Steineck, 1984) and endoparasites of the mountain hare (Burgaz, 1970; Berg, 1981; Soveri and Valtonen, 1983), but neither the blood chemistry nor parasites have been studied with respect to fluctuations in mountain hare populations.

The purpose of this work was to detect the possible effects of population density on condition, blood chemistry and helminth parasitism in mountain hares, and the effects of helminth parasitism on blood chemistry and condition.

MATERIAL AND METHODS

The material consists of three groups of mountain hares (*Lepus timidus*) representing different localities and population densities. Twelve mountain hares were shot in the middle of December 1982 and 12 at the end of February 1983 at Kalajoki (64°15′N, 24°00′E) on the western coast of central Finland (group 1). Both samples were obtained in one day from the same area of < 1 km². Fourteen mountain hares were shot in the middle of December 1982 at Oulu airport, (65°00′N, 25°26′E), about 100 km northeast of Kalajoki (group 2), and 15 hares shot in

242

southern and central Finland during the three previous winters were taken to form group 3. Population densities were estimated from the regional hunting statistics. Snow depth was measured in the same periods and general observations were recorded on the quantities and qualities of forage available to the hares.

Blood samples were taken into heparinized Vacutainer® tubes (Becton-Dickinson and Co., Rutherford, New Jersey 07070, USA) by cardiac puncture immediately after shooting. The plasma was separated out by centrifugation and frozen at −40 C for 3 to 6 months. The hares were weighed and aged (adult or juvenile) by radiography of the distal epiphyseal cartilage of the radius and ulna (Soveri et al., 1986). The abdominal fat was weighed and categorized into four groups according to Soveri et al. (1988; 1 = over 20 g and 4 = no fat).

The lungs, stomach and intestines were examined for parasites. Lesions in the lungs of groups 1 and 3 were categorized (0–3) according to Soveri and Valtonen (1983), but the lungs of the hares in group 2 could not be examined. Macroscopic and stereomicroscopic examinations were made of the contents and walls of the stomach and intestines and the numbers of intestinal helminths were counted. Intensity is described as the mean number of parasites per hare examined.

Plasma chemistry profiles were obtained after thawing the samples. Calcium and magnesium concentrations were determined by atomic absorption spectrophotometry (Perkin-Elmer 2380, Perkin-Elmer Corp., Norwalk, Connecticut 06859, USA), alkaline phosphatase (EC 3.1.3.1) and gamma glutamyl transferase (EC 2.3.2.2) activity according to the recommendations of the Scandinavian Society for Clinical Chemistry and Clinical Physiology (1974, 1976), and urea concentrations enzymatically (Talke and Schubert, 1965), as also cholesterol (Allain et al., 1974). Triglycerides were assayed by an enzymatic method (Wahlefeld, 1974) modified by Boehringer Mannheim GmbH (Mannheim, Germany), creatinine was determined kinetically by a colorimetric method (Fabiny and Ertigshausen, 1971) and total protein was determined by the biuret method (Weichselbaum, 1946).

Differences between the groups (1–3) in the weight and condition of the hares and the intensity of parasite infection were analysed using the Kruskal-Wallis (K-W) test. If a particular variable differed significantly between the age groups, the test was performed separately on the juveniles and adults, otherwise the age groups were pooled. Two-way analysis of variance was used to study the effects of age and group on blood parameters. Because of the fairly high variances in some parameters, logarithmic transformation was performed on all the variables. Multiple regression analysis was employed to study the possible effects of the nematodes *Trichostrongylus retortaeformis* and *Protostrongylus pulmonalis* on blood parameters and the body weight of the hares. In addition to the intensity of parasites, sex, age and season were used as discrete independent variables to check their effect on the relationship between parasites and blood parameters. The regression analysis for body weight had body length as an additional independent variable, since weight is largely determined by the general size of the individual. Blood parameters and parasite intensities were log-transformed.

RESULTS

According to the annual bag records (Fig. 1), the number of hares shot in Kalajoki reached a peak during the winter of 1982-83 and declined steeply the following year. Marks of overbrowsing could already be found in December, such as the bark of growing trees had been eaten in many places, and these marks were clearly visible in February. Snow depth was 5 to 10 cm in December and 50 to 60 cm in February. The situation was very much the same in Oulu region except that the vegetation was different, lacking dwarf shrubs but containing more larger shrubs. The hares in group 3 were from populations of stable and rather low density.

Since the sexes did not differ on any parameter studied (Kruskal-Wallis, $P > 0.05$), they were pooled except for multiple regression analysis. The fat index did not differ between the adults and juveniles (Table 1), and thus the combined material was used to determine the differences between the groups in this respect, which were statistically highly significant (K-W = 26.6, $P < 0.001$; most fat in group 3 and least in group 1). Two-way ANOVA was used to determine the effect of age and place of origin on eviscerated carcass weight. Weight (Table 1) differed between the groups (F = 3.4, $P = 0.04$; highest in group 2 and lowest in group 1). The adults were heavier than the juveniles (F = 7.5, $P = 0.01$). No interaction between age and origin was detected. The weights of the

gastro-intestinal tracts (F = 8.7) and the ratio of intestinal weight to body weight (F = 8.0, Table 1) differed highly significantly between the groups (P < 0.001; highest in group 1 and lowest in group 3) and the amount of wood in the gastro-intestinal contents (Table 1) almost significantly (K-W = 0.7, P = 0.06; highest proportion in group 2 and lowest in group 3). Age did not have any effect on these parameters.

The blood chemistry results and the effects of age and origin on the blood parameters are given in Table 2. Ca, Mg, alkaline phosphatase and creatinine were highest in group 2 (two-way ANOVA). All interaction terms were non-significant (P > 0.05). The effects of sex, age, season and abundance of parasites on the blood characteristics and weight of the hares in group 1 are given in Table 3. The significant regression models show Ca, Mg, triglycerides and cholesterol to be higher in Feb-
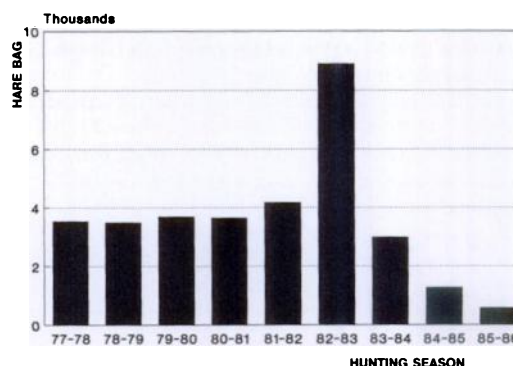

FIGURE 1.   Mountain hare bag at Kalajoki and Alavieska on the west coast of central Finland.

ruary than in December, while the adult hares had lower Mg concentrations and alkaline phosphatase activities and higher body weight than the juveniles.

The parasites collected were the nematodes *Trichostrongylus retortaeformis* and *Protostrongylus pulmonalis* and the cestode *Mosgovoyia pectinata*. The hares

TABLE 1.   Mean fat index (1–4, 4 = no fat), body weight (kg, alimentary tract excluded), weight of stomach and intestines (g), ratio of intestinal weight to body weight and proportion of wood in the total gastro-intestinal contents (%) of mountain hares representing different age groups and data sets.

	Juvenile			Adult		
	n	x̄	SD	n	x̄	SD
Group 1						
Fat	11	3.45	0.69	13	3.31	0.95
Weight	11	2.40	0.28	13	2.64	0.33
Intestinal weight	11	678	135	13	662	120
Intestinal weight/ body weight	11	0.29	0.06	13	0.25	0.06
Wood in alimentary tract	11	39.6	14.6	13	45.0	16.2
Group 2						
Fat	10	2.30	0.48	4	2.00	0.82
Weight	10	2.67	0.25	4	2.90	0.16
Intestinal weight	10	612	63	4	638	35
Intestinal weight/ body weight	10	0.23	0.03	4	0.22	0.01
Wood in alimentary tract	10	44.5	16.2	4	61.2	14.4
Group 3						
Fat	11	1.64	0.67	4	2.50	0.58
Weight	10	2.50	0.32	4	2.76	0.24
Intestinal weight	10	490	97	4	538	85
Intestinal weight/ body weight	10	0.20	0.05	4	0.20	0.03
Wood in alimentary tract	9	27.2	22.8	4	37.5	32.0

TABLE 2. Blood characteristics (mean and SD) of mountain hares representing different age groups and data sets. The ANOVA column shows the significant factors in a two-way analysis of variance performed on each characteristic ($P < 0.05$).

	Juvenile			Adult			
	n	x̄	SD	n	x̄	SD	ANOVA
Calcium (mmol/1)							
Group 1	9	3.2	0.48	11	3.3	0.29	Group ($P = 0.016$)
Group 2	7	3.6	0.29	4	4.0	1.10	
Group 3	10	3.3	0.43	4	3.1	0.45	
Magnesium (mmol/1)							
Group 1	9	1.41	0.234	11	1.33	0.249	Group ($P = 0.001$)
Group 2	7	1.73	0.216	4	1.90	0.608	
Group 3	10	1.42	0.256	4	1.36	0.153	
Alkaline phosphatase (IU/1)							
Group 1	6	144	81.6	8	65	34.1	Age ($P = 0.001$)
Group 2	6	168	87.4	3	119	37.1	
Group 3	9	137	70.0	3	38	23.5	Group ($P = 0.05$)
Gamma glutamyl transferase (IU/1)							
Group 1	5	23	24.2	9	13	6.7	
Group 2	5	19	14.4	3	6	3.4	
Urea (mmol/1)							
Group 1	9	4.8	3.02	11	3.5	2.40	
Group 2	10	2.9	1.73	4	4.7	2.95	
Group 3	11	4.8	2.58	4	6.4	5.39	
Triglycerides (mmol/1)							
Group 1	7	0.63	0.406	8	1.05	0.381	
Group 2	7	1.05	1.005	4	0.95	0.266	
Cholesterol (mmol/1)							
Group 1	9	0.51	0.189	11	0.50	0.206	
Group 2	8	0.56	0.144	4	0.44	0.172	
Creatinine (μmol/1)							
Group 1	9	112	21.2	11	95	21.5	Group ($P = 0.022$)
Group 2	10	129	18.7	3	137	29.9	
Group 3	11	111	56.2	4	92	12.6	
Total protein (g/1)							
Group 1	8	58	10.9	9	59	6.4	
Group 2	9	60	5.6	4	58	10.7	
Group 3	11	53	7.9	4	54	5.4	

in group 1 which were heavily infected with *P. pulmonalis* had higher Ca values than those with little or no infection, and those which were heavily infected with *T. retortaeformis* had lower creatinine concentrations and alkaline phosphatase activities (Table 3). The prevalences and intensities of *T. retortaeformis*, *M. pectinata* and *P. pulmonalis* infection are shown in Table 4. The juveniles were more often infected with *M. pectinata* than the adults (K-W = 3.8, $P = 0.05$). Age did not have any effect on *P. pulmonalis* or *T. retortaeformis* infection, but when the ages were combined the intensities of *P. pulmonalis* were higher in group 1 than in group 3 (K-W = 6.3, $P = 0.01$). There was a significant difference between the groups in *T. retortaeformis* infection (K-W = 7.7, $P = 0.02$; highest intensities in group 1),

TABLE 3.   Regression model predicting blood characteristics and body weight (alimentary tract excluded) of mountain hares in group 1. Sex, age and collection season (December or February) and abundance of the helminths *Trichostrongylus retortaeformis* (TR) and *Protostrongylus pulmonalis* (PP) were used simultaneously as independent variables. Body length was used as an additional independent variable in the analysis of body weight.

Dependent variable	Independent variables	Coeff.	t	P	R^2
Calcium ($n = 20$)	Season	0.34	2.5	0.022	0.52
	PP	0.19	2.5	0.025	
Magnesium ($n = 20$)	Age	−0.20	2.4	0.029	0.53
	Season	0.36	4.2	0.001	
Alkaline phosphatase	Age	−55.1	2.7	0.022	0.76
($n = 14$)	TR	−40.0	4.4	0.001	
Triglycerides ($n = 15$)	Season	0.56	3.2	0.007	0.44
Cholesterol ($n = 20$)	Season	0.22	2.9	0.009	0.32
Creatinine ($n = 20$)	TR	−8.32	2.6	0.017	0.28
Body weight ($n = 23$)	Length	0.03	3.3	0.003	
	Age	0.26	2.8	0.012	0.69
	Season	−0.43	4.9	<0.001	

and the intensities of this and *P. pulmonalis* were much higher in February than in December in group 1 (K-W = 12.9, P < 0.001 for *T. retortaeformis*, and K-W = 5.4, P < 0.02 for *P. pulmonalis*).

DISCUSSION

It seems that population density had some effects on the condition of the mountain hare (Table 1) and the intensities of *P. pulmonalis* and *T. retortaeformis* parasitization (Table 4) if there was a lack of good-quality food. The hares in dense populations (groups 1 and 2) had to eat more poor quality food than those in the normal population (group 3), and this was reflected in high intestinal weights, large amounts of wood in the gastro-intestinal contents and a small amount of abdominal fat (Table 1). It is evident that the nutritive value of the diet of group 1 decreased during the winter because of overbrowsing, and the hares probably had to begin feeding on plants or parts of plants which they do not usually accept because of harmful constituents (Tahvanainen et al., 1985) or poor

TABLE 4.   Number of infected hosts (N) and intensities of helminths (mean and SD per hare examined, scale from 1 to 3 used for *P. pulmonalis*) among mountain hares representing different age groups and data sets.

	Juvenile			Adult		
	N/n	$\bar{x}$	SD	N/n	$\bar{x}$	SD
Trichostrongylus retortaeformis						
Group 1	8/11	1,214	2,127	12/13	2,821	4,379
Group 2	6/10	202	563	2/4	838	992
Group 3	5/9	444	643	2/4	13	24
Protostrongylus pulmonalis						
Group 1	10/11	2.1	0.9	13/13	2.3	0.7
Group 3	3/6	1.0	1.3	2/4	1.5	1.0
Mosgovoyia pectinata						
Group 1	1/11	0.4	1.2	0/13		
Group 2	2/10	0.5	1.3	0/4		
Group 3	2/9	1.0	2.1	0/4		

digestibility (Pehrson, 1980) or for other reasons (Aarnio, 1983). The diameter of the twigs selected for food increased (Aarnio, 1983) and thus more wood was eaten. This kind of diet contains less protein and more cell wall constituents (Aarnio, 1983) which reduce its digestibility.

The elevation of magnesium and calcium in group 1 during the winter (Table 3) may have been the result of changeover to a diet rich in these minerals. The dwarf shrubs favoured by hares in early winter such as *Vaccinium myrtillus* and *Calluna vulgaris*, are lower in Mg and Ca than the trees and shrubs available and eaten by them in late winter (Aarnio, 1983). The hares in group 2, which did not have dwarf shrubs in their environment, already had higher Mg and Ca values in December. Different feeding habits may explain the higher Mg value in the plasma of the young hares in group 1. Soveri et al. (1988) found higher Mg values in the bones of young mountain hares than in those of adults, possibly for the same reason. The higher concentration of triglycerides and cholesterol in February is most probably a reflection of starvation, as the mobilization of body fat by excessive lipolysis results in an increased concentration of these components at least in some other animal species (Bartley, 1989). The higher plasma creatinine concentration in the hares in group 2 suggests greater muscle mass (Finco, 1989), as they were the heaviest hares but did not have the greatest fat reserves. The lower alkaline phosphatase activity in the adult hares was to be expected, as this is known to decrease when animals reach adulthood (Kramer, 1989).

The parasites seem to have fairly minor effects on the blood characteristics of the hares (Table 3). The effect of *T. retortaeformis* in reducing alkaline phosphatase activity may be due to some kind of inhibition of growth and osteoblastic activity because of serious infection and a possible lack of energy, whereas the increase in Ca in the presence of heavy infection by *P. pulmonalis* and the decrease in creatinine brought about by heavy *T. retortaeformis* infection are difficult to explain. One can accept that *T. retortaeformis* infection resulted in a decrease in muscle mass and thus in creatinine, and although it seems that this species had no clear effect on body weight (Table 3), it may have led to a slow decrease in body proteins and thus in muscle mass without having any effect on plasma total proteins or fat reserves.

Trichostrongylus retortaeformis is a common parasite of hares in Finland, particularly when the population is dense (Soveri and Valtonen, 1983), and group 1 had the highest intensities of infection by both it and *P. pulmonalis*. A high density of host animals favours the transmission of parasites, and poor condition may reduce host resistance. The hares in group 2, although originating from a dense population, had a fairly low level of *T. retortaeformis* infection, perhaps partly because they were in better condition. Another possible reason for this difference between groups 1 and 2 may be that the infection pressure on group 2 may have been much lower due to differences in the climate, vegetation etc. Both the prevalence and intensity of infection were very high in February in group 1, but the reason for this is unclear. It may have been due to increased ingestion of infective larvae by the hares or the maturation of inhibited intestinal larvae. The winter is so cold in this area that it is impossible for *T. retortaeformis* eggs to develop into infective larvae, but such larvae could have survived from autumn under the snow and been found by the hare when digging for plants under the snow. On the other hand, it is known that mountain hares seldom dig for food under the snow (Pulliainen, 1972). Inhibited larval development is known to occur in some parasitic nematodes in cattle (Fabiyi and Copeman, 1989) and in the snowshoe hare (Keith et al., 1985), but there are no reports of it involving *T. retortaeformis*. Even so, this could still be the most likely explanation for the increase in prevalence during the winter. The activation

of arrested larvae may be of seasonal origin, as in the snowshoe hare, or it may be due to the poor condition of the animals. When the host is in poor condition, the best strategy for inhibited larvae may be to mature and produce their eggs before the host dies.

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