Gastrointestinal nematodes depress food intake in naturally infected reindeer

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SUMMARY

Models have predicted that directly transmitted macroparasites may influence the abundance of forage plants in herbivore grazing systems by reducing the food intake of their host. Evidence of parasite-induced alterations in host food intake is, however, limited mainly to sheep, cattle and laboratory rodents. We estimated the effect of naturally acquired parasite infections on the appetite of reindeer. Food intake was significantly lower in infected reindeer compared to animals in which the parasites had been experimentally removed. Among the infected animals there was a significant negative relationship between intensity of the directly transmitted macroparasites (i.e. gastrointestinal nematodes) and mean food intake, indicating that the lower food intake was caused by these parasites. The time-specific onset of depression in food intake is also consistent with seasonality in the pathogenic effect from gastrointestinal nematodes. This shows that parasite-induced changes in herbivore food intake is not restricted to agricultural systems, and implies that parasites may have impact on the dynamics of a wide range of herbivore plant communities.

Key words: reindeer, food intake, parasites , grazing system dynamics.

INTRODUCTION

The severe crashes in rabbit populations caused by the *myxomatosa* virus in Great Britain during the 1950s was followed by a change from grassland to woodland. This is a dramatic example of how pathogens of herbivores have influenced the structure of plant communities (Dobson & Crawley, 1994). Less dramatic effects have been suggested by mathematical models showing that directly transmitted macroparasites have the potential to influence the stability of plant-herbivore communities (Grenfell, 1988, 1992). Gastrointestinal nematodes, directly transmitted macroparasites of herbivores, frequently depress the appetite (i.e. food intake) in ruminant hosts like sheep and cattle in a density-dependent manner, i.e. more severely with higher parasite loads (reviewed by Symons, 1985 and Thompson, 1990). In the case of constant host density, Grenfell (1988) showed that gastrointestinal nematodes can stabilize plant abundance in an otherwise overgrazed system through the action on host food intake. Removal of parasites may cause overgrazing and collapse of an initially stable herbivore–plant system.

Grenfell's (1988) model may apply to a variety of ruminant grazing systems. However, with the exception of one study reporting the effect of experimental nematode infections on appetite in red deer (*Cervus elaphus* (L.)) (Johnston *et al.* 1984), information about the relationship between nematode parasitism and ruminant appetite is limited to observations from sheep and cattle. Furthermore, the animals studied typically experienced high transmission rates that characterize modern agricultural grazing systems (Symons, 1985; Thompson, 1989). There is a paucity of data from naturally occurring infections in ruminants that are phylogenetically distant from sheep and cattle and kept in grazing systems widely different from modern agricultural ones. Experiments showing that grazing system structure profoundly influences how the hosts are affected by parasitism (Hansen, Nansen & Foldager, 1984; Reinecke, 1994), coupled with the possible confounding effect of phylogenetical differences on ecological relationships (Nee, Read & Harvey, 1995), stress the need to fill this gap of data.

The semi-domesticated reindeer *Rangifer tarandus tarandus* (L.) herding in Fennoscandia represents an appropriate contrast to modern intensive sheep and cattle grazing systems, as the system is characterized by extensive land use and seasonal migrations (Skjenneberg & Slagsvold, 1968). Reindeer are also phylogenetically distant to ovides and bovines. Additionally, exploring effects of gastrointestinal nematodes in semi-domesticated reindeer may give information about how these parasites affect wild reindeer. This paper describes an experiment designed to test whether naturally acquired nematode infections depress appetite of semi-domesticated reindeer. In the experiment, food intake of reindeer harbouring naturally acquired parasite infections was compared to the appetite of reindeer in which the parasites had been removed by anthelmintic treatment.

Table 1. Estimated abundance (mean number of transmission propagules/g faeces/host ± standard error) and prevalence (number of positive hosts/number of hosts examined) of gastrointestinal nematode eggs in the control (C) and treated (T) group, from October to June

(*, 1 week after anti-parasite treatment.)

	Abundance		Prevalence	
Time	C	T	C	T
Oct.	83·9 ± 21·0	58·7 ± 17·8	8/8	9/9
Nov.	22·6 ± 5·4	30·9 ± 9·6	8/8	8/8
Dec.*		0·0		0/9
Dec.	35·3 ± 8·6	0·0	8/8	0/9
Jan.	20·1 ± 6·7	0·0	8/8	0/9
May	6·3 ± 2·4	0·2 ± 0·1	7/8	2/6
June	9·3 ± 3·3	3·0 ± 1·0	7/7	5/6

MATERIALS AND METHODS

In October we obtained 18 female reindeer calves with natural parasite infections from herds in Northern Norway. We divided them into 2 groups of 9 after an acclimation period of 3–4 weeks. Allocation was done by block randomization based on live weight and parasite burden (i.e. an index of the density of nematode eggs and coccidia oocysts and the presence of cestode eggs in faeces). There were no significant differences in body weight or parasite index between the two groups (ANOVA, $F(1,16) = 0{\cdot}0$, $P > 0{\cdot}8$ and $F(1,16) = 0{\cdot}4$, $P > 0{\cdot}5$, respectively).

In November we removed parasites in the treated group with the anthelmintic ivermectin (1 ml subcutaneous injection, Ivomec 1%; Merck, Sharp & Dome), and gave those in the control group a placebo (1 ml of 0·9% saline). Ivermectin treatment reduces infection levels of gastrointestinal nematodes and arthropods significantly (Campbell, 1983; Nordkvist *et al.* 1983; Haugerud, Nilssen & Rognmo, 1993). In our animals nematode eggs disappeared from faeces in the treated group for at least 2 months after the anthelmintic was given (Table 1). Additionally, nematode abundance (mean number per animal examined) was significantly lower in the treated than in the control group at the end of the experiment (Table 2). The arthropods *Hypoderma tarandi* (L.), *Cephenomya trompe* (Modeer) and *Linguatula arctica* (Riley, Haugerud and Nilssen) were also absent from the treated animals (Table 2).

We measured food intake from November to the end of the experiment, in June, when the animals were slaughtered and parasite intensities estimated. Additionally, throughout the experimental period we weighed the animals, measured rectal temperature as an indicator of significant viral and bacterial infections, and estimated the density of nematode eggs, cestode eggs, coccidia oocysts and larvae of the nematode *Elaphostrongylus rangiferi* (Mitskevich) in faeces (see Fig. 1).

The reindeer were kept in individual enclosures, except from February to early May when they were kept in groups of 2–5. All conditions were designed to be as equal as possible between the animals, and they were fed *ad libitum* a concentrate ration, RF-80 (Stormøllen, Trondheim, Norway, 11·8–14·3% crude protein, Kjeldahl-N), and obtained water in tubs or snow from the ground. From time of treatment to the end of April the ground was covered with snow, and the risk of new infections of gastrointestinal nematodes was negligible. During the last 6 weeks of the experiment, the probability of transmission of nematode larvae increased, as some vegetation became available to the animals.

We examined the faecal samples with a modified McMaster and an extraction method (Halvorsen & Wissler, 1983). Intensities of nematodes in the abomasal contents were estimated as described by Bye (1987). We digested the contents and mucosa of the small intestine and the abomasal mucosa in 1% HCl and estimated the number of nematodes by

Table 2. Abundance (mean number of parasites per examined host ± standard error) and prevalence (number of positive hosts/number of hosts examined) of gastrointestinal nematodes, *Hypoderma tarandi* larvae, *Cephenomya trompe* larvae and *Linguatula arctica* in the control (C, $n = 8$) and treated (T, $n = 6$) group, at the end of the experiment

(Abundance of gastrointestinal nematodes was significantly lower in the treated than in the control group ($F(1,12) = 19{\cdot}7$, $P < 0{\cdot}001$.)

Gastrointestinal nematodes				*Hypoderma tarandi*				*Cephenomya trompe*				*Linguatula arctica*			
Abundance		Prevalence		Abundance		Prevalence		Abundance		Prevalence		Abundance		Prevalence	
C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T
5265 ± 1954	443 ± 212	8/8	6/6	74 ± 20	0	8/8	0/6	7 ± 3	0	5/8	0/6	1 ± 0	0	8/2	0/6

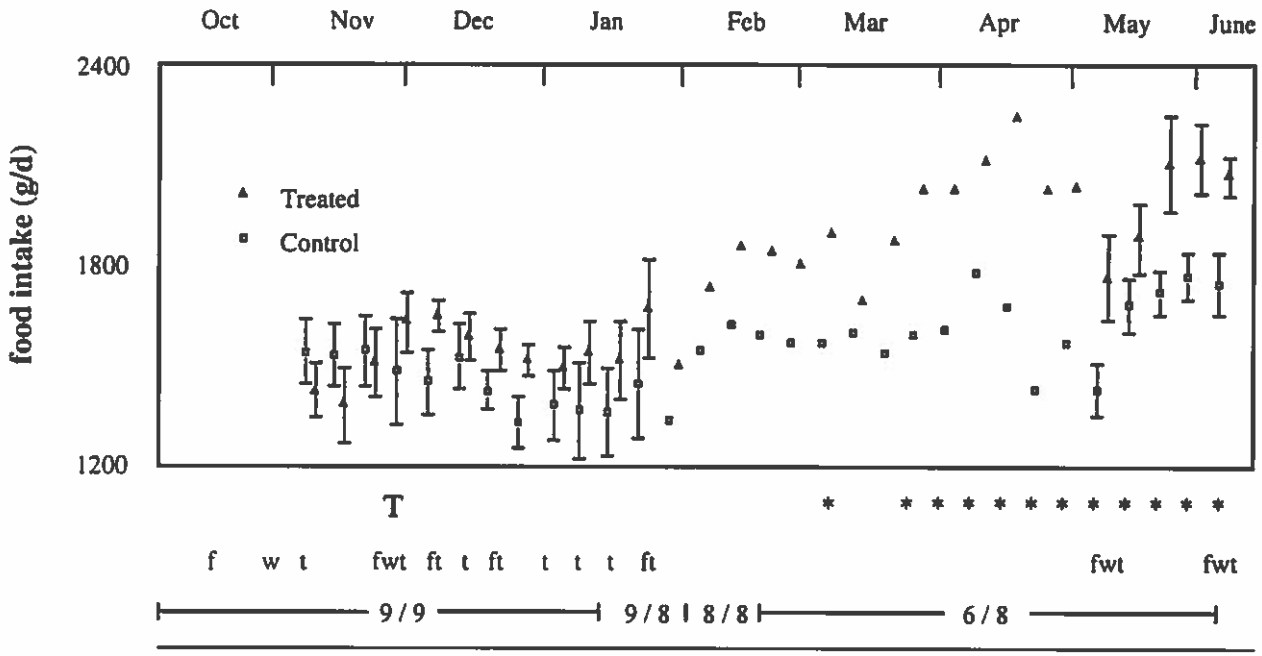

Fig. 1. Mean daily food intake (g/day ± standard error) each week in the control and the treated group from November to June. Food intake was measured from groups, not individuals, from February to the beginning of May. Individually measured food intake was analysed by using repeated measures ANOVA, controlling for initial body weight. Groupwise food intake measurements were analysed with a Students *t*-test and mean variance from the periods of individual measurement was used as an estimate of variance. T, time of treatment against parasites *, weeks with significant differences between the groups in food intake ($2{,}32 < t(12) < 3{\cdot}96$, $F(1,11) = 7{\cdot}25$, $P < 0{\cdot}05$ as opposed to the weeks with no significant difference; $0{\cdot}45 < F(1,14) < 1{\cdot}32$, $1{\cdot}40 < t(12\text{–}15) < 1{\cdot}88$, $0{\cdot}05 < P < 0{\cdot}5$); f, faecal samples taken; w, animals weighted and t, rectal temperature measured. Group sizes are shown as number in treated group/number in control group.

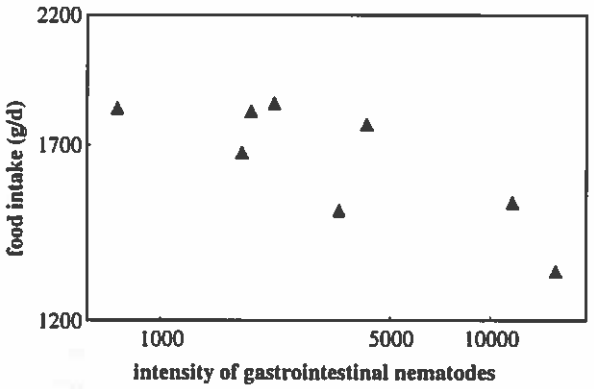

Fig. 2. Figure showing the significant negative correlation between intensity of naturally acquired gastrointestinal nematodes and mean food intake during the period from May to June in the control group of reindeer ($F(1,6) = 11{\cdot}77$, $P = 0{\cdot}01$, adjusted $R^2 = 0{\cdot}61$). The observations are plotted on logarithmic scales.

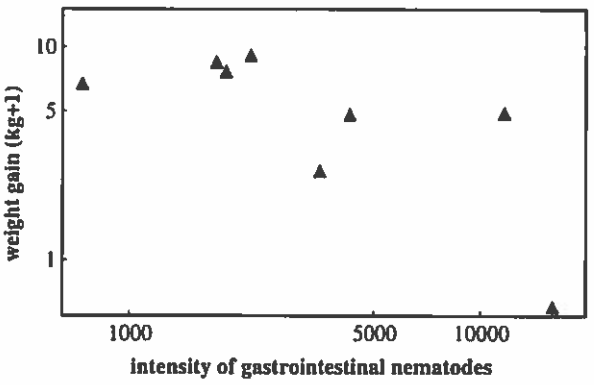

Fig. 3. Figure showing the significant negative correlation between intensity of naturally acquired gastrointestinal nematodes and weight gain from November to June in the control group of reindeer ($F(1,6) = 6{\cdot}45$, $P = 0{\cdot}04$, adjusted $R^2 = 0{\cdot}44$). The observations are plotted on logarithmic scales.

using the method employed for the abomasal contents. Numbers of *H. tarandi*, *C. trompe* and *L. arctica* were counted in the subdermal tissue, pharyngeal pouch and nasal cavities, respectively. Persons recording the data did not know the group identity of the animals. Four reindeer died during the experiment (see Fig. 1), but the other animals appeared in good condition. Intensities of gastrointestinal nematodes were log(10) transformed prior to analyses. Two-tailed probabilities are reported throughout, and means are given with ± standard error.

RESULTS

Food intake was lower in the control group, and a significant difference was apparent during the last 3 months of the experiment (Fig. 1). Mean food

Table 3. Estimated abundance (mean number of transmission propagules/g faeces/host ± standard error) of coccidia oocysts and *Elaphostrongylus rangiferi* larvae and prevalence of cestode eggs (number of positive hosts/hosts of samples examined) in faecal samples from the control (C) and treated (T) group, respectively, at various times.

(Mann Witney U-tests and chi-square tests with Yate's correction were used to test for differences in abundance and prevalence respectively between the two groups. Only 1 of 15 tests of these parameters from the time of treatment to the end of the experiment yielded a significant between-group difference (abundance of coccidia oocysts in December, adj $Z = 2{\cdot}1$, $P < 0{\cdot}05$, $n = 17$).)

	Coccidia		Cestode		*E. rangiferi*	
	Abundance		Prevalence		Abundance	
Time	C	T	C	T	C	T
Oct.	10·7 ± 8·7	4·8 ± 3·5	2/8	3/9	0·0	0·0
Nov.	0·3 ± 0·1	0·3 ± 0·2	3/8	5/8	0·0	0·0
Dec.	0·4 ± 0·2	0·0 ± 0·1	2/8	4/9	0·0	0·0
Jan.	1·2 ± 0·8	0·5 ± 0·3	1/8	5/9	18·3 ± 10·3	2·0 ± 1·6
May	0·2 ± 0·1	0·2 ± 0·1	0/8	0/6	72·5 ± 39·1	44·0 ± 21·0
June	0·8 ± 0·3	2·0 ± 0·8	0/7	1/6	12·1 ± 9·1	7·8 ± 3·9

consumption correlated negatively with gastrointestinal nematode intensity in the control group in the last part of the experiment (Fig. 2). However, there were no such correlations with intensities of the other parasites removed by the treatment (*H. tarandi*; $t(6) = 1{\cdot}4$, $P > 0{\cdot}2$, *C. trompe*; $t(6) = -0{\cdot}1$, $P > 0{\cdot}9$, *L. arctica*; $t(6) = -0{\cdot}4$, $P > 0{\cdot}7$, Spearman rank correlation). Weight gain from time of treatment to the end of the experiment tended to be lower in the control animals (3·0 ± 1·0 kg in the control and 7·4 ± 0·9 kg in treated group, ANOVA; $F(1,12) = 2{\cdot}5$, $P < 0{\cdot}15$). Weight gains correlated negatively with nematode intensity in the control group (Fig. 3), but not with intensities of *H. tarandi*, *C. trompe* or *L. arctica* ($t(6) = -0{\cdot}1$, $P > 0{\cdot}9$, $t(6) = -0{\cdot}2$, $P > 0{\cdot}8$ and $t(6) = -0{\cdot}1$, $P > 0{\cdot}8$, respectively, Spearman rank correlation).

The abundance of coccidia oocysts or *E. rangiferi* larvae or prevalence of cestodes did not differ between the two groups of reindeer (Table 3). Rectal temperature did not differ between the two groups (Dec.–Jan.; $F(1,14) = 0{\cdot}7$, $P > 0{\cdot}4$, Jan.–June; $F(1,11) = 0{\cdot}1$, $P > 0{\cdot}7$, repeated measures ANCOVA with mean pre-treatment values as covariat)

DISCUSSION

Food intake in naturally infected reindeer was lower than in the animals where the parasites had been removed by ivermectin treatment. This difference was, however, significant only during the last 3 months of the experiment. In this period the control group consumed 20% less than the treated group, suggesting that naturally acquired parasite infections have considerable impact on appetite in female reindeer calves.

A diverse group of parasites has been observed to reduce host food intake, including viruses, bacteria, protozoa, helminths and insects (Hart, 1988; Symons, 1985). If the parasites that are not susceptible to ivermectin had higher abundance or prevalence in the control group, they could have caused the difference in food intake. However, as judged from faecal counts of parasite transmission stages neither the abundance of coccidia and *E. rangiferi* nor the prevalence of cestodes was consistently higher in the control group. Additionally, when viruses and bacteria elicit anorexia, fever is frequently observed along with the depression in appetite (Hart, 1988). A higher frequency of fever in the control group is not indicated from measurements of rectal temperature, indicating that the difference in food intake between the two groups was caused by the ivermectin treatment.

Because the degree of depression in food intake depends on intensity of infection, there should be a negative correlation between food intake and intensity of the parasites that caused the food intake reduction. The strong negative correlation between food intake and nematode intensity and the lack of such correlation with the other parasites removed by the treatment, suggest that the gastrointestinal nematodes depressed food intake in the control group. Also, seasonality in nematode biology is consistent with the observation that parasites started to depress reindeer food intake in late winter. Gastrointestinal nematode larvae of ruminants typically lay dormant in the mucosa (i.e. hypobiosis)

Table 4. Gastrointestinal nematode abundance in semi-domesticated reindeer

(Underestimation of nematode abundance in other studies probably explains why the highest abundance was recorded in this study. In none of the other studies were hibernating larvae in the mucosa counted, and in some of them only the abomasum was examined (*, only abomasum examined; **, abomasum and small intestine examined). Reindeer were sampled in spring (S), autumn (A) or late-winter (L-W). References are: (1) present study, (2) Nesbakken (1987), (3) Nordkvist *et al.* (1983), (4) Tollefsen 1983, (5) Rehbinder & von Szokolay (1978) and (6) Nordkvist *et al.* (1984).)

Age and sex (sample size)	Method	Abundance	Reference
Female calf (8)	**, S	5279	(1)
Male 1·5 years (64)	*, A	4700	(2)
Male and female calf (6)	**, L-W	3770	(3)
Male and female all age (55)	**, A	1600	(4)
Male and female all age (54)	*, A	360	(5)
Male and female calf (5)	**, L-W	60	(6)

Table 5. Effect of ivermectin treatment on body weight of semi-domesticated reindeer

(Relation to season is given as time of treatment–time of measurement. *; ANOVA on their data; males; $F(1,12) = 3{\cdot}9$, $P = 0{\cdot}07$, females; $F(1,14) = 0{\cdot}7$, $P = 0{\cdot}4$. References are: (1) Oksanen *et al.* (1992), (2) Heggstad *et al.* (1986), (3) Nordkvist *et al.* (1984), (4) Nordkvist *et al.* (1983) and (5) Oksanen *et al.* (1993).)

Age and sex of animals (sample size) and time	Effect on body weight	Reference
Male and female adult (92), Dec.–April	Treatment efficacy increased gains	(1)
Male and female calf, female adult (385), Nov.–Nov.	Higher weight	(2)
Male and female calf, (54), Nov.–April	Males gained more, not females	(3)
Male and female calf (30), Feb.–April	Males gained more, not females*	(4)
Female adult (61), Dec.–June	No effect on treated animals	(5)

in autumn and mid-winter, and mature in late winter and spring (Armour & Duncan, 1987), and the parasites' effect on food intake normally tracks this seasonality (Enterocasso *et al.* 1986). Thus, gastrointestinal nematodes seem to have had a particular effect on reindeer appetite in this experiment.

Three points support that the result obtained from captive female calves is also valid for free-ranging semi-domesticated reindeer in general. First, nutrition modifies the effect parasites have on food intake. That is, malnourished hosts have more severely depressed appetite for a given parasite burden (Holmes, 1987). The reindeer in this experiment were offered food with a higher protein content than normally consumed by free-ranging reindeer (Skjenneberg & Slagsvold, 1968). Hence, nematodes should be more likely to depress appetite in free-ranging reindeer than in those consuming the protein-rich diet of this experiment.

Second, the abundance of gastrointestinal nematodes in the control group of this experiment was typical of that found in other studies of parasites in semi-domesticated reindeer. Gastrointestinal nematode abundance is generally higher in adults than in calves (Rehbinder & von Szokolay, 1978; Tollefsen, 1983), and males are probably more susceptible to parasites than female reindeer (Folstad *et al.* 1989). This implies that female calves have lower intensities of gastrointestinal nematodes than reindeer from other age and sex groups.

Third, weight gains and food intake were both negatively associated with intensities of gastrointestinal nematodes in our reindeer. We therefore assume that an effect of gastrointestinal nematodes on reindeer body weight also implies an effect on appetite. Parasite removal increased body weight of calves and adult semi-domesticated reindeer of both sexes in other studies, indicating that parasite-

modulated food intake is not restricted to female calves. The lower body weight in untreated reindeer could have been caused by gastrointestinal nematodes, but also by other parasites, in particular those also removed by the treatment. However, by using two anti-parasite treatment regimes that differ in efficacy against nematodes and act identically against arthropod parasites, Oksanen *et al.* (1992) found that weight gain decreased with decreasing efficacy against nematodes. This indicates that nematodes have a particular negative effect on body weight. Also, body weight seems to be more severely depressed in males than in females, supporting the assumption that gastrointestinal nematodes have a larger impact on appetite in other groups of semi-domesticated reindeer than the one studied here. In sum, our results seem to apply to semi-domesticated reindeer.

Our results also have implications for wild reindeer grazing systems. In such systems parasites may influence the plant–host interaction by regulating host population density (Grenfell, 1992). For parasites to regulate a host population, however, their effect on host reproduction and/or survival must depend on host population density (Anderson & May, 1978). Coupling the negative correlations between nematode intensity and food intake or weight gains from this study with a positive correlation between abomasal nematode abundance and population density in wild reindeer (Bye, 1987) may give a positive correlation between pathogenicity of nematode infections and reindeer population density. In the parasite removal experiment of Oksanen, Nieminen & Soveri (1993) in semi-domesticated reindeer where the treatment had no effect on the body weight of adult females, there was a tendency for the calves of untreated females to have lower body weight after the summer grazing period. This parallels a key density-dependent effect in the regulation of reindeer population size; at high density calves are lighter in autumn than calves from low-density areas leading to density dependence in both mortality and future fecundity of the calves (Skogland, 1983, 1990). Such effects have been accrued to food limitation (Skogland, 1983, 1990), and one might speculate that parasites interact with malnutrition amplifying the effect of food limitation. Similar patterns have been observed in the soay sheep (*Ovis aries*) at the island of St Kilda (Gulland, 1992). The fact that parasite-induced changes in herbivore food intake is not restricted to agricultural systems, suggests that pathogens of herbivores may have impact on a wide range of plant communities.

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