GASTROINTESTINAL NEMATODES OF MOOSE (*ALCES ALCES*) IN RELATION TO SUPPLEMENTARY FEEDING

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ABSTRACT: Winter supplementary feeding of wildlife is controversial because it may promote parasite and disease transmission by host aggregation. We investigated the effect of winter supplemental feeding of Scandinavian moose (*Alces alces*) on gastrointestinal (GI) parasite infection in two counties of southern Norway by comparing fecal egg counts of moose using, and not using, feeding stations between January 2007 and March 2010. We identified three different GI nematodes based on egg morphology. All three were found in Hedmark county while in Telemark county we found only *Trichuris* sp. (prevalence 33%). Prevalence of Trichostrongylidae (65%) and *Nematodirus* sp. (26%) in Hedmark was not affected by feeding station use. However, the probability of infection varied significantly between years sampled (Trichostrongylidae) and age class (*Nematodirus* sp.). Fecal egg counts (FEC), a proxy for intensity of infection, of Trichostrongylidae were higher in the year when winter weather conditions were more challenging and prevalence was higher, and decreased with increasing body mass. Adult moose had higher FECs than did juvenile moose, and female juveniles had lower abundances than did male juveniles. Use of feeding stations did not affect probability of infection with any of the nematodes or intensity of infection with Trichostrongylidae. We discuss our findings in terms of parasite life histories and recommend that parasitologic surveillance be included in the monitoring of feeding programs.

Key words: Deer, GI nematode, moose, supplemental feeding, wildlife management.

INTRODUCTION

Parasite transmission occurs by direct or indirect contact between hosts. Therefore, processes which increase contact rates, such as increases in population density or host aggregation, have the potential to promote parasitic diseases (Gortázar et al., 2006; Body et al., 2011). As supplementary feeding of wildlife can lead to unnaturally high local population densities and levels of contact between hosts (Peek et al., 2002), it is a controversial management practice with implications for parasite transmission within wildlife and between wildlife and domestic livestock (Cross et al., 2007).

Supplementary feeding of game animals during winter, as practiced throughout Europe and parts of North America, is carried out for many reasons (Putman and Staines, 2004). These include increasing over-winter survival, improving body weight or trophy sizes, increasing reproductive performance and fertility, improving the annual hunting yield, and for other recreational opportunities like viewing and photographing. In addition, diversionary feeding may reduce or prevent agricultural or forest damage (Gundersen et al., 2004) or help prevent traffic accidents on main highways and railways (Andreassen et al., 2005). Effects on body condition and reproduction are equivocal, varying with feeding regime, type of supplementary feed provided, and location of the feeding site (Putman and Staines, 2004), while unnaturally dense winter populations around feeding stations can have negative consequences that include habitat damage (van Beest et al., 2010a; van Beest et al., 2010b) and the potential for increased disease transmission (Hines et al., 2007). This includes bacterial and viral pathogens as well as endoparasites including gastrointestinal (GI) nematodes.

Parasite infections in wildlife, as in domestic animals, often have sublethal effects (Gunn and Irvine, 2003), including reduced appetite (Arneberg et al., 1996) and food assimilation (Coop and Kyriazakis, 2001), that lead to poorer competitive ability, reduced resistance to other pathogens, impaired growth, and poorer reproductive success (e.g., Stien et al., 2002; Newey and Thirgood, 2004; Hughes et al., 2009). These in turn can impact the population dynamics of both host and parasite populations (Albon et al., 2002). Gastrointestinal nematodes are abundant in wild ruminants (Hoberg et al., 2001) and typically have subclinical effects such as those described above (Gunn and Irvine, 2003).

The exposure and susceptibility of elk (*Cervus elaphus*) in the Greater Yellowstone ecosystem (United States) to GI nematode infection was influenced by supplementary feeding (Hines et al., 2007). However, elsewhere, little is known about how supplementary feeding of large herbivores affects parasitism. Supplementary feeding of moose (*Alces alces*) with silage (bales of mixed graminoids) is practiced in Norway to reduce train and vehicle collisions (Andreassen et al., 2005) and in an attempt to limit moose damage to forestry during winter (Gundersen et al., 2004). In this study, we investigated the GI parasites of Norwegian moose and compared individuals that used supplementary forage with those feeding on natural browse. Our main goal was to determine whether there was a difference in prevalence and intensity of parasite infections in relation to feeding site use. We tested two alternative hypotheses: H1) Winter supplementary feeding enhances parasite transmission by aggregating moose at feeding grounds, leading to higher parasite abundances in feeding-site users; or H2) supplementary feeding improves body condition, enabling moose to better combat parasite infection, leading to lower parasite abundances in fed moose.

MATERIALS AND METHODS

Study areas

We carried out our study at two sites, one centered in Skien and Siljan municipalities in Telemark county, southern Norway (59°21'N, 9°38'E), and the other in Stor-Elvdal municipality, Hedmark county in southeastern Norway (61°24'N, 11°7'E; Fig. 1). Both areas harbored large moose populations. The landscape-scale winter density of moose was approximately 1.3 moose/km² in both study areas (Milner et al., 2012) while local wintering area densities far exceeded this. Hunting was the main cause of moose mortality in both study areas, as large predators were absent in Telemark and only occasionally present within the Hedmark study area.

In Hedmark, supplementary feeding of moose started in the late 1980s (Andreassen et al., 2005) while in Telemark feeding began 4 yr prior to our study (van Beest et al., 2010b). During the 4- to 6-mo-long winter, approximately 1,700 tons and 150 tons of supplementary forage were consumed by moose in Hedmark and Telemark, respectively (van Beest et al., 2010a; van Beest et al., 2010b). The longer duration and greater extent of the feeding program in Hedmark meant that a larger proportion of the moose population used feeding stations than in Telemark, with an average adult female spending 20.4 (±2.7)% of time within 100 m of a feeding station in Hedmark but only 2.0 (±0.6)% in Telemark (Fig. 2). An estimated 47% of the population's winter forage requirements were met by silage in Hedmark and about 23% in Telemark (Milner et al., 2012).

The climate differed between the study areas, being colder in the more-continental Hedmark area. Average daily minimum and maximum January temperatures during the study were −2.2 C and 3.1 C, respectively, in Telemark, and −15.5 C and −8.3 C, respectively, in Hedmark. Snow cover lasted from December to April in Hedmark and for a slightly shorter period in Telemark, with mean February snow depths of 68 cm and 73 cm, respectively.

Parasite sampling

Fecal samples were collected from the rectum of immobilized adult female moose and their calves in Telemark in January 2007 and in Hedmark in January 2009 and 2010 (adults only). The Hedmark individuals were recaptured and resampled in March of the same winter. Ninety-two individuals were sampled. Moose were immobilized from a helicopter using etorphine according to standard
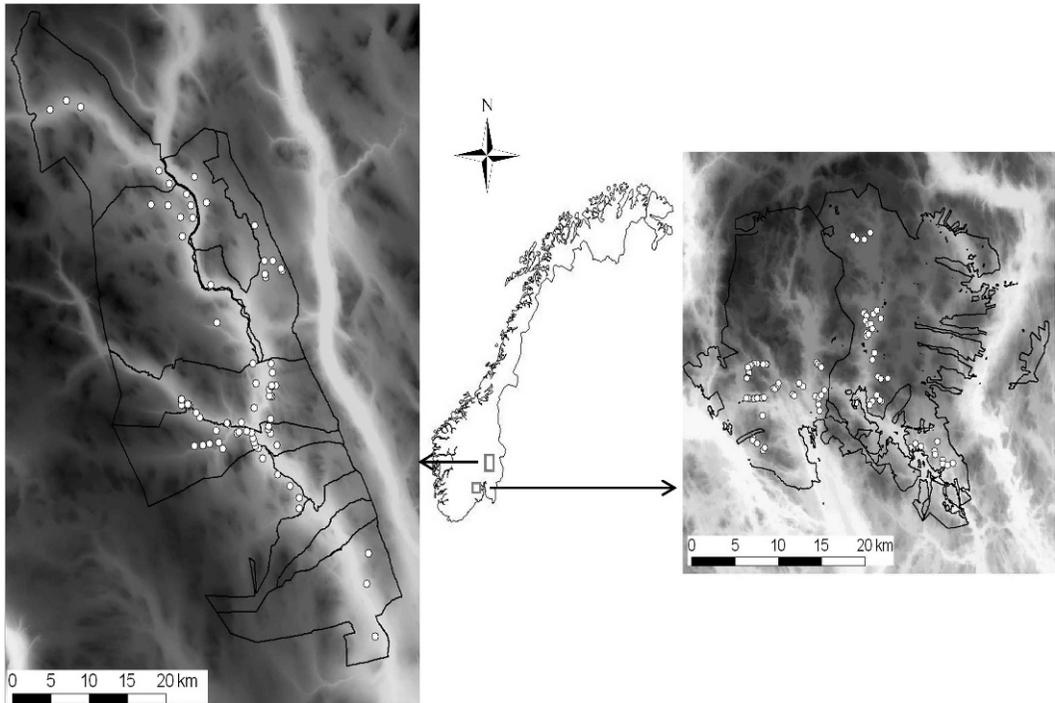
FIGURE 1. Feeding stations (white circles) in the two study sites: Telemark (right) in southern Norway and Hedmark (left) in southeastern Norway. Black lines depict management boundaries and background shows altitude ranging from <100 m (white) to 1,500 m (black).

procedures (Arnemo et al., 2003). Moose were restrained and weighed from the helicopter and adults were fitted with a GPS collar (Tellus Remote GSM, Followit AB, Lindesberg, Sweden). Fecal samples were frozen at −20 C prior to analysis at the laboratory of Finnish Food Safety Authority, Evira in Oulu, Finland (see Discussion section for the implications of freezing). Downloaded GPS positions were used to assign feeding status of the moose (van Beest et al., 2010b). We categorized individuals as low, moderate, and high users with, respectively, ≤5%, 6–25%, and >25% of GPS positions occurring within 100 m of a feeding station (Fig. 2).

Fecal samples were analyzed for parasite eggs using standardized modified McMaster flotation techniques for parasite investigations (Evira LAB 5614/1). We counted eggs per gram of feces (epg) by weighing and homogenizing 3 g of feces in 42 ml lukewarm tap water. The mixture was strained through a 770-µm aperture sieve, and 12.5 ml of the solution was centrifuged at 300 × G for 3 min. The supernatant was discarded, and saccharose (density 1.25 g/ml) was added to the sediment to a total volume of 2.5 ml. After careful mixing, the solution was pipetted into a
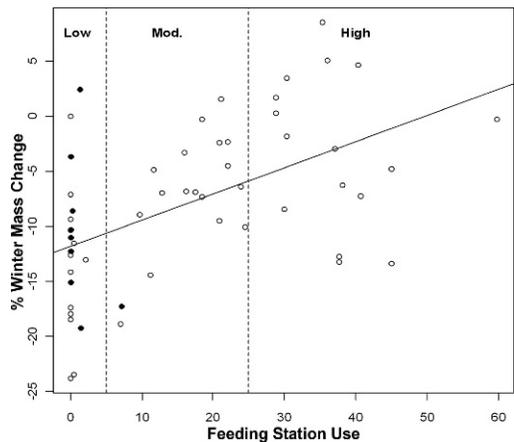

FIGURE 2. Percentage winter mass change (100*[January mass–March mass]/January mass) in relation to feeding station use among adult female and juvenile moose (*Alces alces*) in two study sites: Telemark, southern Norway (*n*=10; closed circles) and Hedmark, southeastern Norway (*n*=46; open circles). The percentage of time spent within 100 m of feeding stations was used as an index of feeding station use, categorized as low (≤5%), moderate (6–25%), and high (>25%).

chambered McMaster slide. Parasite eggs were counted using a microscope with 100× magnification (10× ocular, 10× objective) and categorized based on morphologic features (Soulsby, 1982). Using this method, every egg found represented 20 epg.

We explained the patterns of parasite distribution within the moose populations in terms of prevalence and intensity of infection (abundance) and examined factors affecting the probability of infection. Prevalence was the number of moose infected/number of moose examined. We used fecal egg counts (FEC) as a proxy for intensity of parasite infection, being the mean epg of a particular parasite in all the hosts examined (i.e., infected+uninfected; Margolis et al., 1982). Probability of infection was the likelihood that a fecal sample or an individual was infected.

Statistical analysis

We compared the prevalence of nematodes between groups using binomial proportions tests. In Hedmark, where we had two samples from many individuals, we tested whether month affected the probability that a fecal sample was infected by using generalized linear mixed models with binomial errors, a logit link, and moose identification number fitted as a random factor. As the probability did not differ between months in any of the cases, we focused on factors affecting the probability that an individual was infected, considering an individual to be infected if either the January or March sample was positive. We used generalized linear models with binomial errors and a logit link. The explanatory variables were year, age class, feeding status, and mean body mass (kg) averaged over January and March. We made separate models for each parasite in each study area.

We investigated the possibility of coinfection with the two predominant parasites found in Hedmark by correlation, but found it not statistically significant (correlation coefficient=0.024). Furthermore, the frequency distributions of Trichostrongylidae and Nematodirus sp. were so dissimilar that fitting models of coinfection abundance was not warranted (Grafen and Woolhouse, 1993).

In addition, we ran models of factors affecting FEC of Trichostrongylidae in Hedmark. We investigated the effect of age class, feeding status, body mass, month, and year (both fitted as two-level factors), and their 2-way interactions, using a negative binomial distribution with a log link function. Again, we fitted moose identification as a random effect. We then ran models for adults and calves

separately; we included the effect of sex when running models for calves only. Due to the low prevalence and, hence, large number of zeros for both Nematodirus sp. and Trichuris sp., we did not analyze factors affecting the FECs of these parasites.

We used backward stepwise selection from a starting model, including all variables and their interactions. In all analyses the significance level was set to $P \leq 0.05$.

RESULTS

We found three morphologically different types of GI nematode eggs in feces; Trichostrongylidae, Nematodirus sp., and Trichuris sp. All three were found in Hedmark while in Telemark we only found Trichuris sp. Trichostrongylidae eggs could not be indentified to genus or species.

In line with H2, feeding station use affected moose body condition in late winter (Milner et al., in press). Body mass at the start of the winter did not differ in relation to feeding station use in either study area ($F_{2,66}=1.77$, $P=0.179$), suggesting that use of feeding stations was not dependent on body condition. By late winter, there were marked differences in mass such that over-winter mass change differed significantly in relation to feeding station use ($F_{2,52}=9.67$, $P<0.001$) with low, moderate, and high feeding-station users losing 12, 7, and 3% of their January body mass, respectively (Fig. 2).

Prevalence

Parasite prevalence varied from 0% to 80% depending on nematode, study site, month, and year (Table 1) but did not differ with feeding status (Table 2). In Hedmark, 51 of 68 (75%) individuals, and in Telemark 8 of 24 (33%) individuals were infected with at least one GI parasite. Overall prevalence of Trichostrongylidae infection was 65% in Hedmark and zero in Telemark. Prevalence in Hedmark differed between years ($\chi^2=5.67$, $P=0.017$), being 78% in 2009 and 46% in 2010. Prevalence of Nematodirus sp. was zero in Telemark, while in Hedmark it tended to differ between months, being 28% in January

TABLE 1.   Prevalence (%) of gastrointestinal nematodes in moose (*Alces alces*) in the Hedmark and Telemark study areas in southern Norway in relation to age class, month, and year of sampling.

Study site	Age class	Month	Year	*n*	Trichostrongylidae	*Nematodirus* sp.	*Trichuris* sp.
Hedmark	Adult	January	2009	19	74	11	3
		January	2010	14	29	29	0
		March	2009	16	75	6	0
		March	2010	18	39	11	0
	Calf	January	2009	19	65	45	0
		March	2009	10	80	20	0
		March	2010	9	33	11	0
Telemark	Adult	January	2007	14	0	0	27
	Calf	January	2007	9	0	0	44

and 11% in March ($\chi^2=3.8$, $P=0.051$). *Trichuris* sp. only occurred in one sample in Hedmark, an adult female that used feeding sites heavily (prevalence=1%). In Telemark, the prevalence of *Trichuris* sp. was 33%; however, with only one infected and one uninfected moderate users of feeding stations, we could not test for a difference in relation to feeding station use.

Probability of infection

We found no evidence to suggest that feeding station use affected the probability of infection with any of the parasites. In Hedmark, individuals were more likely to be infected with Trichostrongylidae in 2009 than in 2010 ($\chi^2=8.47$, $P=0.004$), but feeding status had no significant effect ($\chi^2=0.08$, $P=0.959$). The probability that an individual in Hedmark was infected with *Nematodirus* sp. tended to be higher among calves than adults ($\chi^2=3.39$, $P=0.065$). In Telemark, the probability of infection with *Trichuris* sp. was not

significantly affected by body mass, age class, or their interaction ($P>0.05$).

Intensity of infection

The range of FEC was 0–80, 0–540, and 0–180 epg for *Nematodirus* sp., *Trichuris* sp., and Trichostrongylidae, respectively. The intensity of infection ranged from 4.55 epg in *Nematodirus* sp. to 170.0 epg in *Trichuris* sp. (Table 3).

In Hedmark, FECs of Trichostrongylidae were significantly affected by age class, year, and body mass ($\chi^2=4.22$, 14.80, 6.26, and $P=0.04$, <0.001, 0.012, respectively; Fig. 3, Table 3). Adult moose had higher FECs than did juveniles. Both adult and juvenile moose had lower Trichostrongylidae egg counts in 2010 than in 2009, and egg counts decreased with increasing body mass. Differences in egg counts with feeding status and month (Table 3) were not statistically significant ($P=0.226$ and $P=0.411$, respectively). Within adults only, moose had higher

TABLE 2.   Prevalence (%) of gastrointestinal nematodes in moose (*Alces alces*) in the Hedmark and Telemark study areas in southern Norway in relation to feeding station use, categorized as low, moderate, or high with individuals spending, respectively, ≤5%, 6–25%, and >25% of their time within 100 m of a feeding station.

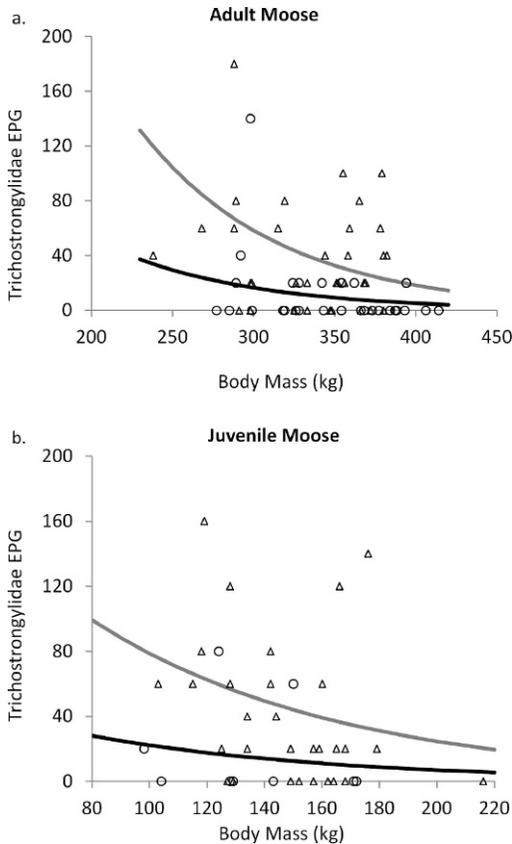| Study site	Feed use	*n*	Trichostrongylidae	*Nematodirus* sp.	*Trichuris* sp.
Hedmark	Low	17	71	35	0
	Moderate	21	57	19	0
	High	20	70	20	5
Telemark	Low	22	0	0	32
	Moderate	2	0	0	50
	High	0	-	-	-

FIGURE 3. Predicted fecal egg counts in eggs per gram (EPG) of Trichostrongylidae for a) adult and b) juvenile moose (*Alces alces*) in 2009 (grey line) and 2010 (black line), and observed values (2009 triangles and 2010 circles) in Hedmark, southeastern Norway. Note different scales for body mass.

Trichostrongylidae FECs in 2009 ($\chi^2 = 11.39$, $P<0.001$), and egg counts decreased with increasing body mass ($\chi^2 = 4.02$, $P=0.045$, Fig. 3a). Within juveniles, female moose had lower Trichostrongylidae FECs than did male juvenile moose ($\chi^2 = 6.79$, $P=0.047$), and egg counts decreased with increasing body mass ($\chi^2 = 10.30$, $P=0.03$; Fig. 4).

DISCUSSION

As far as we are aware, this is one of the first studies of GI parasites in moose in Scandinavia since the pioneering work of Nilsson (1971; see also Nikander, 1989). Based on egg morphology, we found three gastrointestinal nematode groups; Trichostrongylidae, *Nematodirus* sp., and *Trichuris* sp. Contrary to our hypotheses, supplementary feeding had no effect on the prevalence or probability of infection with any of these nematodes, nor on the intensity of Trichostrongylidae infection. The occurrence of the parasites differed between the two study sites. Trichostrongylidae and *Nematodirus* sp. were both absent in Telemark, while the prevalence of *Nematodirus* sp. in Hedmark and *Trichuris* sp. in both areas was relatively low. Trichostrongylid populations of moose may contain parasites of domestic ruminants or other cervids. However, as seen in Sweden (Nilsson, 1971) and Finland

TABLE 3. Mean fecal egg counts (±standard error) (eggs/gram feces) from moose (*Alces alces*) as a proxy for intensity of infection with gastrointestinal nematodes in relation to feeding station use in Telemark, southern Norway (2007) and in Hedmark (2009 and 2010), southeastern Norway. Feeding station use was categorized as low, moderate, or high with individuals spending, respectively, ≤5%, 6–25%, and >25% of their time within 100 m of a feeding station.

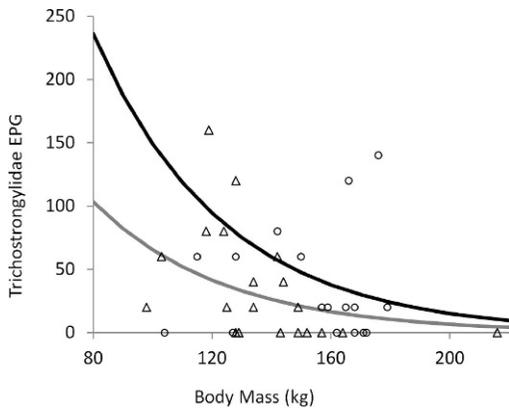| Year	Feed use	n	Trichostrongylidae	*Nematodirus* sp.	*Trichuris* sp.
2007	Low	22	0	0	55.5 (28.3)
	Mod.	2	0	0	170 (170)
	High	0	-	-	-
2009	Low	18	35.6 (10.2)	8.89 (4.35)	0
	Mod.	14	32.9 (11.6)	4.29 (3.09)	0
	High	23	55.7 (8.80)	7.83 (3.92)	0.87 (0.87)
2010	Low	11	16.4 (7.54)	9.09 (4.95)	0
	Mod.	22	5.45 (1.94)	4.55 (2.92)	0
	High	8	27.5 (17.7)	7.50 (7.50)	0

FIGURE 4.   Predicted fecal egg counts in eggs per gram (EPG) of Trichostrongylidae in moose (*Alces alces*) calves in Hedmark, southeastern Norway. (Predicted lines: gray=females, black=males. Observed points: triangles=females, circles=males).

(Nikander, 1989), moose GI parasites are mostly species-specific. Both authors found the same two predominant species of trichostrongylids. These were reported as *Ostertagia leptospicularis* and *Spiculopteragia alcis* by Nilsson (1971) and as *Ostertagia antipini* and *Spiculopteragia dagestanica* by Nikander (1989); however, *O. leptospicularis* and *Mazamastrongylus dagestanica* are now considered the valid names for these two species (Hoberg et al., 2001).

Fecal egg counts were generally low. Nilsson (1971) reported that the GI worm burdens of moose were almost always low. However, in the case of Trichostrongylidae, our low FECs were probably influenced by the fact that we froze the fecal samples while awaiting laboratory examination (samples were collected primarily for dietary analysis). The formation of ice crystals during freezing may have ruptured the thin-walled shells of Trichostrongylidae eggs, as reported in other strongyle eggs (Nielsen et al., 2010), decreasing their ability to float and, hence, be detected. Consequently, our FECs of Trichostrongylidae are likely under-estimates. However, as samples from all moose were handled in the same way, this was unlikely to have introduced a bias with

respect to individual covariates such as feeding station use.

As our samples had low egg counts, there was a chance that low-intensity infections remained undiagnosed using the McMaster technique, although the scaling factor in our modification, in which every egg seen represented 20 epg, was lower than the 50 epg often used (e.g., Hansen and Perry, 1994). Furthermore, when modeling the probability of infection, we considered an individual to be infected if at least one sample had a positive egg count. This reduces the chance that false negatives have affected our results. A better FEC method might have been the modified Wisconsin centrifugation technique, which can detect one egg in 8 g of feces (Cox and Lemiski, 1989). When dealing with low or very low FECs, such added sensitivity may enable subtle differences between groups to be demonstrated.

The overall parasite prevalence in moose in our study was higher than that found in elk by Hines et al. (2007). In North America, 49% of fecal samples from elk in the Greater Yellowstone ecosystem were infected with at least one GI nematode as compared with an overall prevalence (both study sites) for moose in our study of 64%. Our results concur with those of Hines et al. (2007) regarding increasing FECs of GI nematodes from January to late winter–early spring, although month was not significant in our intensity of infection models, any effect being masked by a decrease in body mass between January and March (Milner et al., in press). However, unlike Hines et al. (2007), we found no effect of feeding status on FECs.

As with most parasitic nematodes, GI nematodes have direct life cycles (Newey et al., 2005). After being defecated with fecal pellets, eggs undergo several larval stages, and infective larvae are incidentally ingested by host animals while feeding on vegetation (Soulsby, 1982). In *Trichuris* sp., larval development occurs within the egg, which is highly resistant to the environment (Soulsby, 1982). On the other

hand, development to the infective stage is slow, requiring probably two summers, as has been found in England with the swine whipworm *Trichuris suis* (Burden and Hammet, 1979). New hosts can be infected by eating eggs of *Trichuris* spp. Typically, under harsh environmental conditions, parasite transmission rates are low in winter (Halvorsen et al., 1999) and larvae undergo arrested development in the abomasal mucosa, maturing in late winter or spring (Armour and Duncan, 1987), although some nematode taxa do shed eggs and show continued transmission during winter in the arctic (Irvine et al., 2000). We do not know the life-history strategies of the nematodes in our study. However, if they follow the strategy typical for harsh winter conditions, we could expect relatively low fecal egg outputs during the winter supplementary feeding season and the development of infective phases during the summer (Hrabok et al., 2006). Such a life history could explain our low FECs and the lack of difference in relation to feeding station use, as infection would occur outside the winter feeding season which ends around the time of snow melt and prior to spring migration. The restart of larval development at the end of winter, or a decrease in immune capacity with declining body condition during winter, could account for a rise in FECs between January and March (Body et al., 2011). Sheep *Nematodirus* spp. and *Ostertagia* (*Teladorsagia*) spp. showed strong overwinter survival on sheep pastures in the vicinity of Oslo, midway between Hedmark and Telemark (Helle, 1971), while reindeer abomasal nematodes also survive winter (Irvine et al., 2000; Hrabok et al., 2006). Therefore, it seems likely that larvae of moose abomasal nematodes could also survive Norwegian winter conditions.

The relationship between FEC and the number of adult worms was unknown and is dependent on both the number and fecundity of adult female worms, host immunity, and seasonal egg shedding patterns, which differ between parasite species (Smith, 1994; Irvine et al., 2000). However, as our primary interest was in detecting differences in FEC in relation to feeding station use within, rather than between, parasites, this would not have affected our main conclusions. The FEC measures parasite activity (reproduction) while worm counts will also show inactive parasites, if present.

The moose is regarded as a strict browser (e.g., Clauss et al., 2006), feeding primarily on the leaves and shoots of tall plants such as trees and shrubs, although during spring and autumn moose feed more on dwarf shrubs such as bilberry (*Vaccinium myrtillus*). The transmission of GI nematodes is generally more challenging within browsers than in grazers such as sheep, which feed on the ground, and is likely a strong contributing factor to the generally low GI parasitism that we observed. Behavioral patterns such as fecal avoidance of contaminated ground (van der Wal et al., 2000) and selective foraging could further explain why we found no support for our hypotheses if moose, like other ungulates, have spatial separation of foraging and rumination bouts and dung deposition (Ezenwa, 2004). Although high densities of fecal pellets were found close to the silage bales (van Beest et al., 2010a), moose generally fed from the top of the bale, well above the ground where fecal matter was lying. Furthermore, larval development of parasites is unlikely during winter, and infective larvae cannot relocate far (Soulsby, 1982).

Adult moose had higher Trichostrongylidae FECs than did calves, while calves had a higher probability of infection with *Nematodirus* sp. Very often parasite loads increase with age (Wilson et al., 2002), although situations in which juveniles have higher parasite burdens than do prime-age adults are regularly reported (Body et al., 2011), presumably due to acquired immunity. Adult moose experiencing poor winter nutrition may invest fewer resources in immunity, prioritizing maintenance

of body protein for survival in the short-term and growth and reproduction in the longer-term (Coop and Kyriazakis, 2001). Such a lack of acquired immunity has been shown in Svalbard reindeer (*Rangifer tarandus platyrhynchus*; Irvine et al., 2000) and red deer (*Cervus elaphus*) in Scotland (Irvine et al., 2006). Our finding that juvenile females had a lower intensity of Trichostrongylidae infection than did juvenile males is typical for mammals with sex-specific differences in immunocompetence (Wilson et al., 2002). *Nematodirus* sp. tend to be strongly immunogenic (Winter, 2002), and *Nematodirus filicollis* worms were more common in young than in old roe deer in Sweden (Nilsson, 1971). The higher prevalence of *Nematodirus* spp. in moose calves than in adults in our study is in line with these findings, although FECs were low in both cases.

While our results showed no effect of supplementary feeding on GI parasite prevalence or intensity of infection, they nonetheless provide important baseline data for future comparisons, and we would recommend that parasitologic surveillance should be included within the long-term monitoring of feeding programs. Furthermore, our study raises awareness of many gaps in our knowledge concerning the life-history strategies of GI nematodes, and their ecologic consequences, in Scandinavian moose. Rising environmental temperature due to climate change has been indicated as a reasonable cause for increases in parasites and other pathogen-related diseases (Murray et al., 2006). A good understanding of parasite life histories and epidemiology in wildlife species may, therefore, become even more important in the future, especially where wildlife management leads to increased host density or aggregation.

ACKNOWLEDGMENTS

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