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Endoparasites in a Norwegian moose (*Alces alces*) population – Faunal diversity, abundance and body condition

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ABSTRACT

Many health surveillance programs for wild cervids do not include routine parasite screening despite evidence that gastrointestinal parasites can affect wildlife population dynamics by influencing host fecundity and survival. Slaughter weights of moose in some regions of Norway have been decreasing over recent decades but any role of parasites has not yet been considered. We investigated parasite faunal diversity of moose in Hedmark, SE Norway, by faecal analysis and identification of adult abomasal and caecal nematodes during the autumn hunting season. We related parasite prevalence and abundance to estimates of body condition, gender and age. We identified 11 parasite groups. Moose had high abomasal gastrointestinal nematode (GIN) burdens and all individuals were infected. *Ostertagia antipini* and *Spiculopteragia alcis* were the most prevalent abomasal GINs identified. *O. leptospicularis* and *Telodorsagia circumcincta* were also identified in the abomasa while a range of other GIN and *Moniezia* sp. eggs, and coccidia, *Dictyocaulus* sp. and Protostrongylid larvae were found in faeces.

Female moose had higher mean abomasal nematode counts than males, particularly among adults. However, adult males had higher faecal egg counts than adult females which may reflect reduction in faecal volume with concentration of eggs among males during the rut. We found no strong evidence for the development of acquired immunity to abomasal nematodes with age, although there was a higher Protostrongylid and *Moniezia* infection prevalence in younger animals. High burdens of several parasites were associated with poor body condition in terms of slaughter weight relative to skeletal size but unrelated to visually evaluated fat reserves. Given findings from earlier experimental studies, our results imply sub-clinical effects of GI parasite infection on host condition. Managers should be aware that autumn faecal egg counts and field assessments of fat reserves may not be reliable indicators of parasitism and may underestimate impacts on wildlife populations.

1. Introduction

The moose (*Alces alces*) is the largest cervid in Norway and an important game species. But despite its high economic, social and cultural value (Storaas et al., 2001) and the role it plays as a keystone species in boreal ecosystems (Speed et al., 2014), little is known about the parasite fauna of moose in Norway. The health surveillance programs for wild cervids in Norway (Solberg et al., 2012; Vikøren et al., 2013) do not include routine parasite screening. This is in spite of evidence from other wildlife that gastrointestinal parasites can affect population dynamics by influencing host fecundity and survival, especially when interacting with factors such as forage availability and predation (Gulland, 1992; Hudson et al., 1992a; Halvorsen et al., 1999; Stien et al., 2002; Sinclair et al., 2007; Hughes et al., 2009).

The Norwegian moose population has increased exponentially since the 1970s as a result of changes in forestry and game management, including the introduction of gender and age specific harvesting strategies (Lavsund et al., 2003). Moose management has focused on maintaining high population densities for hunting whilst minimising damage to forestry and agriculture (Lavsund et al., 2003). However, decreasing slaughter weights have been recorded in a number of regions over recent decades (Wam et al., 2010; Solberg et al., 2012). High densities together with declines in natural forage availability (Milner et al., 2013a; Mathisen et al., 2014), cohort effects (Wam et al., 2010) and climate warming (van Beest and Milner, 2013) may be important explanatory factors, but any role of parasites has

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not yet been considered. Given that climate change is predicted to affect parasite faunal diversity and host–parasite interactions, especially at high latitudes (Kutz et al., 2014), a better understanding of moose parasitism is required for optimal management into the future.

The only previous survey of gastrointestinal parasites in Norwegian moose showed that 75% of individuals had at least one type of gastrointestinal parasite, based on faecal egg counts (Milner et al., 2013b). Strongyle-type eggs were found in 65% of samples and a quarter contained *Nematodirus* sp. eggs. However, further species identification of the strongyle-type eggs requires molecular analysis, carrying out faecal cultures and morphologically identifying L3 larvae or identifying adult nematodes from the gastrointestinal tract. The aims of this study were (1) to investigate parasite faunal diversity of moose using both faecal analysis and identification of adult nematodes from the abomasum and caecum during the autumn hunting season, and (2) to relate parasite burdens to estimates of body condition, as well as gender and age.

2. Materials and methods

2.1. Study area and population

Hedmark county, in south-eastern Norway, is a leading county for moose in Norway (Statistics Norway). In the 2012–2013 hunting season, 20% of the national moose game bag (nearly 35,000 moose) was shot in Hedmark while a quarter of all traffic killed moose also came from this county (446/1724) (Statistics Norway 2014a, 2014b). The area is characterised by boreal forest, dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), with small mixed stands of deciduous species. These forests account for 20% of Norway's commercial forestry resources. Hedmark also has 10% of Norway's total agricultural land, primarily used for livestock production (Rognstad and Steinset, 2012).

Our study was conducted in the municipalities of Stor-Elvdal, Åmot and Tynset in Hedmark county. The climate is continental with 30 year mean summer (May–September) and winter (October–April) temperatures of 10.6 °C and –5.8 °C, respectively. The 30 year mean annual precipitation is 628 mm and the mean snow depth (October–April) is 39 cm (Mathisen et al., 2014). The estimated winter moose population density is around 1.3 moose per km^2 (Milner et al., 2012). Red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) also occur in the area at low densities, while domestic sheep (*Ovis aries*) and cattle (*Bos Taurus*) range freely in forests within the moose range throughout the summer months.

Moose included in this study were shot as part of the licensed hunt between 25th September and 1st November 2013. The potential for hunter selection bias towards good condition individuals was considered to be limited as hunters select for age class, gender and reproductive status in adult females, but given the short and intense hunting season they have little opportunity to select for body condition within these groups (Nilsen and Solberg, 2006). We worked closely with 21 hunting teams who contacted us when an animal had been felled. They provided the GPS coordinates for the location of the gastrointestinal tract removed during carcass dressing. The hunters completed a protocol form for each animal, recording its gender, age class (adult, yearling or calf), dressed carcass weight and a subjective field assessment of cardiac and renal fat reserves (Kistner et al., 1980). Hunters tied off the rectum to avoid contamination with free living nematodes and marked the gastrointestinal tract with an identification label to allow the protocols and digestive tracts to be matched. Blood, milk (where relevant) and the jaw bone were also collected.

Gastrointestinal tracts were located and sampled within 1–12 hours of notification by the hunting teams. The abomasum and caecum were ligated prior to removal and a faecal sample was obtained from the rectum. Faeces and blood were transported refrigerated.

2.2. Gastrointestinal parasites

2.2.1. Abomasum

The abomasum was cut along its greater curvature and the contents washed into a bucket. The internal mucosal wall was washed thoroughly with running water until the volume in the bucket reached 2 l. However where more than 2 l of water was necessary to clean the abomasum sufficiently, the contents in the bucket were allowed to sediment for 30 mins until the supernatant could be siphoned off to the 2 l mark. The sediment and fluid in the bucket were then thoroughly homogenised and two 50 ml subsamples were removed for later counting and species identification of nematodes (tubes A and B). Each 50 ml tube was allowed to stand for 30 mins before the supernatant was removed, taking care not to disturb the sediment. The tube was then refilled with 75% ethanol and frozen at –20 °C to preserve the parasites until counting and identification could take place.

Following thawing, we counted all nematodes in both A and B tubes of all moose. Counts were then multiplied to give an estimated total count (count in 100 ml × 20 to give count in 2 l) for further analysis. The nematodes were divided into male and female for species identification. We identified up to a maximum of 50 male nematodes from tube A to species level for 30 moose. Male nematodes were mounted in polyvinyl lactophenol (Chemi-Teknikk AS, Oslo, Norway) for 2–5 mins in a dorsal position and examined at 20–100× magnification. Species identification was based on the following morphological features: spicules, oesophageal valve length and dorsal ray structure (Drózdz, 1965, 1995; Lichtenfels and Hoberg, 1993).

2.2.2. Caecum

The caecum of all moose was washed as discussed earlier and two 50 ml subsamples were obtained. These were examined for *Trichuris* sp. after sieving the samples through a 1 mm sieve. Any *Trichuris* sp. found on the sieve were stored in 75% ethanol.

2.2.3. Faeces

The abundance of endoparasitic eggs and oocysts was estimated using a modified McMasters method and zinc–chloride/sodium chloride flotation fluid (with a specific gravity of 1.3) (Taylor et al., 2007; Gibbons et al., 2014) with a 3 g faecal sample mixed with 75 ml tap water. A total of 2 ml flotation fluid was examined for eggs giving a theoretical detection limit of 78 eggs per gram (EPG)/oocysts per gram (OPG). Eggs and oocysts were identified to genus level (*Moniezia* sp., *Trichuris* sp., *Nematodirus* sp., and *Eimeria* sp.) and, where possible, species level (*Strongyloides papillosus, Nematodirus battus*), based on morphological characteristics. A number of gastrointestinal nematode (GIN) eggs can only be identified to order, given morphological similarities and size overlap. Therefore *Trichostrongylus* sp., *Haemonchus* sp., *Ostertagia* sp., *Cooperia* sp., *Chabertia* sp., *Oesophagostomum* sp. and *Telodorsagia* sp. were grouped as strongyle-type eggs.

The Baermann technique was used to isolate, quantify and identify parasitic L1 stage larvae in the faeces (Gibbons et al., 2014). A 10 g faecal sample, wrapped in gauze, was suspended for a minimum of 12 hours in tepid water at room temperature. The bottom 10 ml of sediment was aspirated and centrifuged (at 1500 *g* for 5 mins). The supernatant was then aspirated to the 1 ml mark and a 100 µl subsample of the sediment examined at 100× magnification for larvae. The larvae were recorded as hatched GIN larvae, the lungworm *Dictyocaulus* sp. or dorsal spine larvae (DSL, Protostrongylid larvae with an s-shaped tail with spine). The number of larvae per gram faeces (LPG) was estimated from the subsample count (number

of larvae detected in 100 µl × 10/the weight of the faeces in the faecal sample).

2.3. Estimates of body condition

Hunters' subjectively assessed renal and cardiac fat reserves to give a body fat estimate. They categorised 48 individuals as having poor (score of <3), normal (score = 3) or good (score > 3) fat reserves (Kistner et al., 1980; Stephenson et al., 1998) based on criteria shown on the hunter protocol form.

A body condition index (BCI) was estimated for 43 individuals from a linear regression of the natural logarithm of slaughter weight on the natural logarithm of jaw bone length (slope ± SE = 2.40 ± 0.17) with an age and gender interaction included (slope ± SE = 0.05 ± 0.01). Jaw bone length, an index of skeletal body size, was measured (in cm) using a wooden ruler. Individuals were aged by counting the number of annual layers in the cementum of the incisor root tips (Rolandsen et al., 2008). The residuals from the best model ($R^2 = 0.92$, $F_{4,38} = 126.1$, p-value < 0.01) were used as an individual's BCI in subsequent analyses.

2.4. Statistical methods

Parasite diversity, abomasal counts and abundance (a measure of the level of infection in all hosts, including non-infected individuals) of eggs and larvae (Bush et al., 1997) were modelled using generalised linear models (glms) with Poisson errors and a log link function. Age, gender, body condition (BCI), slaughter weight and the interaction between age and gender were fitted as explanatory variables. Age was fitted as a continuous variable but in addition we tested whether age class (3 classes: calf, yearling, adult) had greater explanatory power. Lactation status in adult females was also included in the model of abomasal parasite abundance. The variability in fat reserve score was too low to include. Factors affecting the probability of host infection were determined using glms with binomial errors and a logit link function and the same explanatory variable as earlier. Models were not run for parasites with low numbers of infected hosts (*Trichuris* sp., *Nematodirus* sp., *Dictyocaulus* sp., *T. circumcincta*). All models were selected using backwards selection, with non-significant variables being excluded. We detected overdispersion in some models and corrected the standard errors using quasi-glm models. Significance of terms was assessed by analysis of deviance, using Chi squared tests for glms and the *F*-ratio test for quasi-glms. We investigated the relationship between faecal egg count (FEC) and the number of egg producing adult nematodes to aid interpretation of FEC, a widely used measure of parasite infection. We carried out a Spearman's rank test of the correlation between the adult female abomasal nematode counts and strongyle-type egg counts. All analyses were carried out using R 3.0.1 (R Development Core Team, 2013). A significance level of $p < 0.05$ was used for all analyses.

3. Results

3.1. Study population

A total of 49 abomasa and caeca and 45 faecal samples were collected from the 29 male and 20 female moose included in this study (Table 1). Hunters reported little variation in fat reserves, classifying most individuals as 'normal'. Exceptions were one calf with poor reserves and 7 adults with good reserves. We found no significant correlation between the hunters' estimates of fat reserves and body condition index (Spearman's rank r = 0.14, p = 0.36). The age of adult animals ranged from 2 to 14 years, with a higher average age among females (Table 1). The average dressed carcass weight of yearlings was similar between the sexes, 132 kg for females and 131 kg for males whereas male calves (72 kg) were on average heavier than females (66 kg).

3.2. Parasite faunal diversity

Overall we identified 8 parasite groups by faecal analysis (strongyle-type GIN eggs, *Strongyloides papillosus, Nematodirus* sp., *Trichuris* sp., *Moniezia* sp., *Eimeria* sp., *Dictyocaulus* sp. and DSL; Table 2). Four species of GIN were identified in the abomasum (*Ostertagia antipini, O. leptospicularis* (and the minor morph *O. kolchida*), *Spiculopteragia alcis* and *Telodorsagia circumcincta*) and *Trichuris* sp. was identified in the caecum of one individual (Table 2). Of the 11 parasites identified overall, 6 were found in a single moose, with 10 individuals hosting at least 4 different parasites (Fig. 1). Faunal diversity counts should be considered minima as only up to 50 adult nematodes were identified in each of 30 moose. We found no relationships between parasite diversity and age, sex or body condition of hosts.

Faecal egg counts (n = 45) showed that 82% of the moose had one or more species of GIN eggs (Table 3). Baermann analysis (n = 41) showed that 7% of individuals had *Dictyocaulus* sp. and 22% had Protostrongylidae larvae (DSL) (Table 3). Adult abomasal nematodes were found in all the animals examined (n = 49). *Ostertagia antipini* and *Spiculopteragia alcis* were the most prevalent species occurring in 87% and 80% of sampled moose respectively (Table 2). The number of female abomasal nematodes counted within an individual was positively correlated with its strongyle-type EPG of faeces (Spearman's rank r = 0.424, p = 0.004; Fig. 2).

3.3. Correlates of parasitism

We found evidence of age, gender and body weight or condition effects on the abundance and host probability of infection of several parasites (Table 4). In general, younger animals were more affected by *Moniezia* sp., *Dictyocaulus* sp. and DSL than older animals, while abomasal nematode infection increased with age (Table 4). The probability of infection with *O. antipini* and *S. alcis* was lower

Table 1
The age and gender distribution of moose investigated for gastrointestinal parasites, faecal egg and larval counts during the 2013 hunting season in Hedmark county, Norway, showing mean dressed carcass weight (mass) as well as fat reserves and body condition index (BCI: population mean = 0, BCI < 0 is below average condition, BCI > 1 is above average condition).

Age class	Gender	n	Mean mass (kg) [range]	Fat reserves (n = 48)			Mean BCI (n = 43)	Mean age (years)
				Poor	*Average*	*Good*		
Calf	5 males	10	69 [50–86]	10%	90%	–	–0.049	<1
	5 females						0.038	
Yearling	7 males	10	131 [106–170]	–	100%	–	0.011	>1,
	3 females						–0.068	< 2
Adult	Male	17	198 [160–277]	–	82%	18%	0.019	4.3
Adult	Female	12	167 [137–188]	–	67%	33%	–0.002	6.6

Table 2
Counts and prevalence of adult abomasal nematodes of the genera *Ostertagia, Spiculopteragia* and *Telodorsagia* found in moose in Hedmark, classified by age/gender class from a subset of 30 moose from the overall study population.

Age group	n[a]	Abomasal counts			Prevalence (%)			
		Min	Median	Max	*O. leptospicularis*/*O. kolchida*	*O. antipini*	*S. alcis*	*T. circumcincta*
Calf								
Male	5 – 5	260	980	4,220	40 [10–82][b]	100 [59–100]	60 [18–90]	0 [0–41]
Female	5 – 4	60	290	1,720	25 [0–81]	75 [19–99]	25 [0–81]	0 [0–60]
Yearling								
Male	7 – 7	1320	5,400	11,920	0 [0–41]	86 [42–100]	100 [59–100]	0 [0–41]
Female	3 – 3	1980	3,140	4,300	0 [0–71]	100 [29–100]	67 [10–99]	0 [0–71]
Adult								
Male	17 – 3	1700	7,200	9,520	100 [29–100]	33 [0–91]	100 [29–100]	0 [0–71]
Female	12 – 8	8280	27,730	56,000	38 [9–76]	100 [63–100]	100 [63–100]	13 [0–53]
Total	49 – 30	60	6,720	56,000	30 [14.7–49.4]	86.7 [65.3–94.4]	80 [54.1–87.7]	3.3 [0–17.2]
No. infected/uninfected hosts					9/21	25/5	22/8	1/29

[a] Sample size for abomasal counts – sample size for abomasal nematode species prevalence.
[b] 95% confidence interval for the prevalence.

among males than females, although gender effects on abundance depended on both the parasite and the sample type (Table 4). Parasite abundance or probability of infection increased as body condition or carcass weight decreased in *Eimeria* sp., DSL larvae and abomasal nematodes (Table 4, Fig. 4).

Strongyle-type eggs were detected in all age/gender classes across 64% of individuals, with egg shedding intensity in positive animals

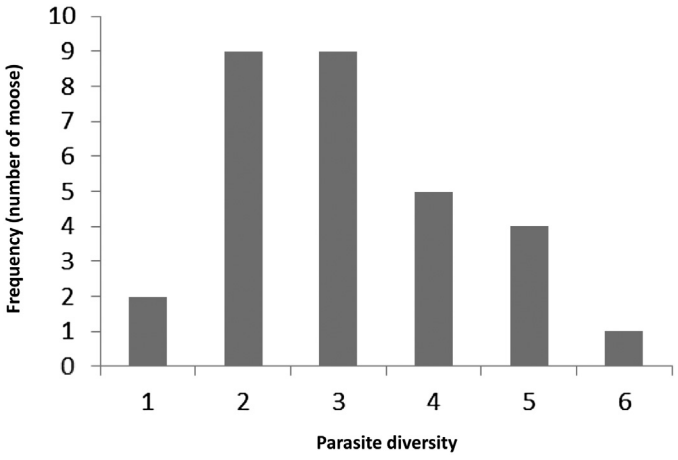

Fig. 1. Histogram of number of parasite groups (parasite diversity) found in individual moose (n = 30) shot during the licensed hunting season, autumn 2013, in Hedmark county, Norway.

(n = 29) varying from 78 to 1716 EPG (mean 199, median 78). Male animals had significantly higher mean strongyle-type EPGs than females even when the one extreme outlier (1716 EPG in a male) had been excluded from the analysis ($F_{1,40} = 4.65$, p = 0.037). EPG also increased with age ($F_{1,40} = 4.43$, p = 0.042) but showed no significant relationship with either body condition or carcass weight (Table 4).

Strongyloides papillosus eggs were detected in 20% of individuals, occurring in all age/gender classes except male calves. The intensity of shedding in positive individuals (n = 9) ranged from 78 to 156 EPG (mean 87, median 78). There were no significant correlates of egg prevalence or abundance. *Nematodirus* sp. and *Trichuris* sp. eggs were detected once each in two different adult males. The prevalence of *Moniezia* sp. was 78% in calves but it was absent in older age classes ($\chi^2_{2,42} = 29.37$, p < 0.001; Table 4). Egg counts decreased significantly with age ($F_{1,35} = 416.9$, p < 0.001) and were higher in female than male calves ($F_{1,35} = 40.70$, p < 0.001, Table 4). *Eimeria* oocysts were detected in all age/gender classes except male yearlings, and shedding in positive individuals (n = 9) ranged from 78 to 1404 (mean 269, median 78). Individuals with low body weights and poor condition had higher *Eimeria* sp. oocyst counts ($F_{1,36} = 6.59$, p = 0.015 and $F_{1,36} = 11.87$, p = 0.001 respectively).

Larval output of DSL ranged from 1 to 85 LPG (mean 32, median 25 LPG) among positive animals (n = 9). Calves and poor condition individuals had significantly higher DSL infection probabilities than older and better condition animals ($\chi^2_{1,38} = 15.83$, p < 0.001 and $\chi^2_{1,38} = 4.19$, p = 0.041 respectively, Fig. 3). Males and light weight individuals had higher mean LPG than females and heavy animals ($F_{1,36} = 15.56$, p < 0.001 and $F_{1,36} = 77.38$, p < 0.001). No larvae of

Table 3
The prevalence (%) of parasite eggs and larvae based on McMaster and Baermann faecal examinations of moose shot during the licensed hunting season, 2013, in Hedmark county. The 95% confidence interval of the prevalence is given in square brackets.

Age class	Strongyle-type	*Eimeria* sp.	*Trichuris* sp.	*Nematodirus* sp.	*Strongyloides* sp.	*Moniezia* sp.	*Dictyocaulus* sp.	DSL
	Eggs	Eggs	Eggs	Eggs	Eggs	Eggs	Larvae	Larvae
Calf	7[a]/9[b]	3/9	0/9	0/9	2/9	7/9	1/9	6/9
	44.4%	33.3%			22.2%	77.8%	11.1%	66.7%
	[19–73%]	[12–65%]	[0–30%]	[0–30%]	[6–55%]	[45–94%]	[20–44%]	[35–88%]
Yearling	6/10	1/10	0/10	0/10	3/10	0/10	2/8	2/8
	60.0%	10.0%			30.0%		25.0%	25.0%
	[31–83%]	[2–40%]	[0–28%]	[0–28%]	[11–60%]	[0–28%]	[7–59%]	[7–59%]
Adult	19/26	5/26	1/26	1/26	4/26	0/26	0/26	1/24
	73.1%	19.2%	3.8%	3.8%	15.4%			4.2%
	[54–86%]	[9–38%]	[1–19%]	[1–19%]	[6–34%]	[0–13%]	[0–14%]	[7–20%]
Total	29/45	9/45	1/45	1/45	9/45	7/45	3/41	9/41
	64.4%	20.0%	2.2%	2.2%	20.0%	15.6%	7.3%	22.0%

[a] No. positive cases.
[b] No. examined.

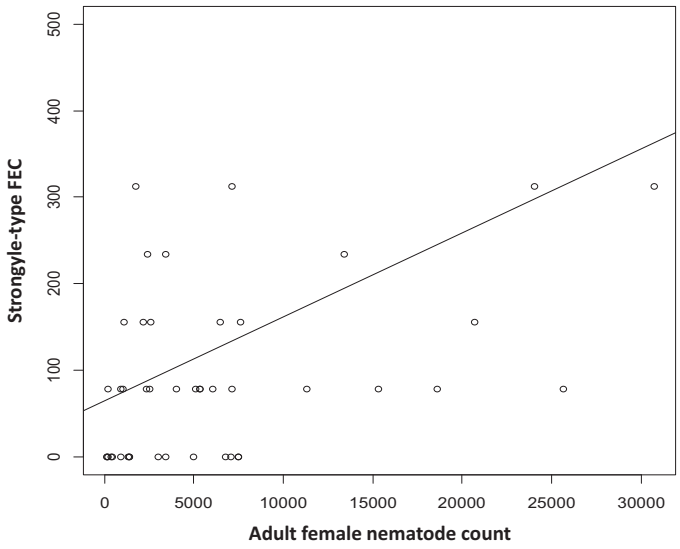

Fig. 2. The correlation between the number of adult female nematodes counted in the abomasa and the Strongyle-type EPG of faeces in moose (n = 45) shot during the licensed hunting season, autumn 2013, in Hedmark county, Norway. Note that 1 extreme outlier with a count of 1716 EPG has not been plotted.

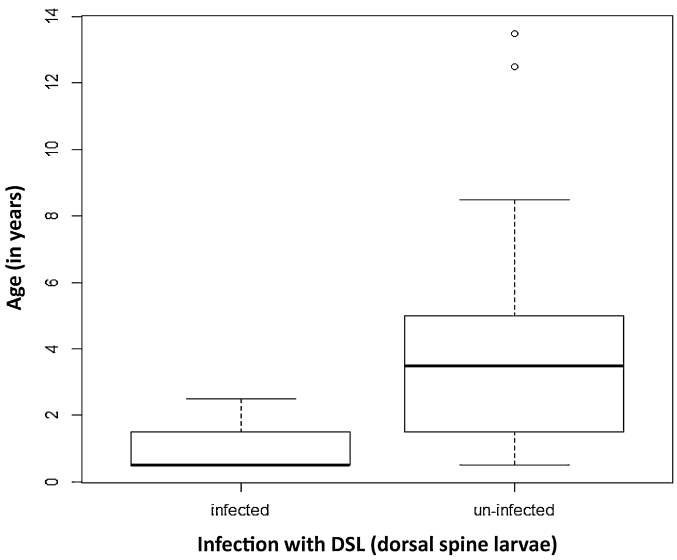

Fig. 3. A box–whisker plot showing the prevalence of infection with protostrongylid larvae (dorsal spine larvae) in moose hunted during the licensed hunting season, autumn 2013, in Hedmark county, Norway, in relation to age. The median (solid black line), quartiles (ends of boxes) with the whiskers indicating the variability outside the quartiles, and extreme outliers, individual points, are shown.

Dictyocaulus sp. were found in adult moose, suggesting an effect of age but this was not tested due to small sample size. Infected individuals also had poorer than average body condition but with only two yearlings and one calf infected, each with fewer than 3 LPG faeces, further investigation is needed.

Among the abomasal nematodes identified, *Ostertagia antipini* prevalence was significantly lower in adult males than in other age/gender classes (interaction: $\chi^2_{1,26} = 8.17$, $p = 0.004$, Table 4). The probability of infection with *Spiculopteragia alcis* was also higher among females than males ($\chi^2_{1,25} = 8.71$, $p = 0.003$) and increased with age ($\chi^2_{1,25} = 17.12$, $p < 0.001$) while it decreased with carcass weight after accounting for age ($\chi^2_{1,25} = 10.58$, $p = 0.001$). *Ostertagia leptospicularis* occurred in calves and adults but was not detected in any yearlings, giving a significant age class effect ($\chi^2_{2,22} = 10.04$, $p = 0.007$). The minor morph *O. kolchida* was detected in one adult only.

Estimated intensity of adult nematode infection ranged from 60 to 56,000 parasites in the total abomasal content (mean 12,540, median 6720). Abomasal parasite burdens (total count) increased significantly with carcass weight of moose, particularly in females (carcass weight–gender interaction: $F_{1,38} = 17.00$, $p < 0.001$, Fig. 4). The three most extreme points (counts above 40,000) were all female. Furthermore, counts increased significantly as body condition decreased ($F_{1,38} = 25.42$, $p < 0.001$, Fig. 4). A closer look at the counts revealed that just over half the animals had counts of 10,000 or fewer nematodes, while ten individuals (20% of the study population) harboured 57% of the total abomasal nematode count. Three of the 12

Table 4
Summary of the significant factors affecting parasite abundance and host probability of infection in a Norwegian moose population, determined by generalised linear models.

Parasite	Abundance				Probability of infection			
	Age	Gender	Mass	BCI	Gender	Age	BCI	Mass
Strongyle-type eggs[a]	* (+)	* (M > F)	ns	ns	ns	ns	ns	ns
Eimeria sp. eggs	ns	ns	* (–)	** (–)	ns	ns	ns	ns
Moniezia sp. eggs	*** (–)	*** (M < F)	*** (+)	ns	ns	*** (C > Y + A)	ns	ns
Trichuris sp. eggs								
Nematodirus sp. eggs								
Strongyloides sp. eggs	ns	ns	ns	ns	ns	ns	ns	ns
Dictyocaulus sp. larvae								
DSL larvae	ns	*** (M > F)	*** (–)	ns	ns	*** (–)	* (–)	ns
Adult abomasal nematodes pooled	ns	[(M < F) *** (+)]		*** (–)				
O. leptospicularis adults					ns	** (C + A > Y)	ns	ns
O. antipini adult worms					[(M < F) ** (–)]		ns	ns
S. alcis adult worms					** (M < F)	*** (+)	ns	** (–)
T. circumcincta adults								

BCI – body condition index; Mass – carcass weight (kg); ns – not significant.
Grey cells indicate models were not run due to too few positive hosts (*Trichuris* sp., *Nematodirus* sp., *Dictyocaulus* sp., *T. circumcincta*), or in the case of adult abomasal nematodes, abundance only being available for all species pooled (probability of infection: 100%).
Direction of effect is given in parentheses (M: males, F: females, C: calves, Y: yearlings, A: adults). Interactions are represented by square brackets.
* $p \le 0.050$.
** $p \le 0.010$.
*** $p \le 0.001$.
[a] Excluding 1 extreme outlier.

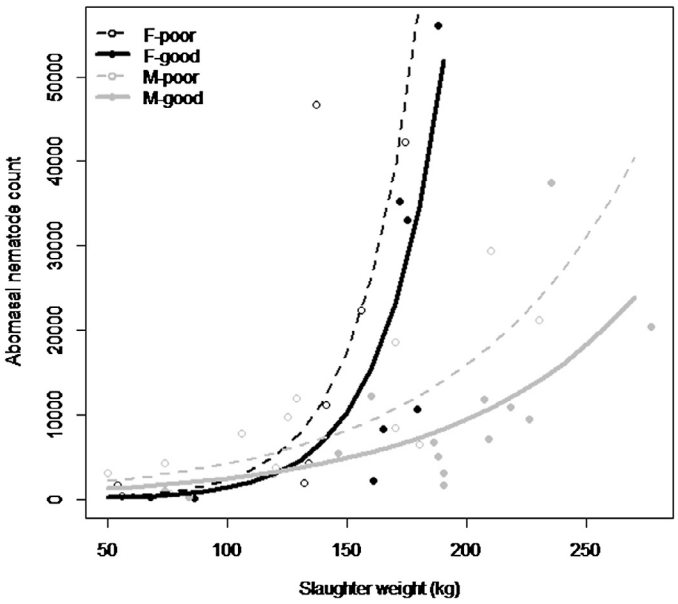

Fig. 4. Counts of abomasal nematodes in moose, hunted during the licensed hunting season, autumn 2013, in Hedmark county, Norway, in relation to slaughter weight, gender (F – females [black]; M – males [grey]) and body condition index (poor – BCI < 0 [open circles]; good – BCI > 0 [filled circles]). The lines show model predictions from a quasi-Poisson generalised linear model explaining 72.4% of the deviance. The lines show the model predictions for individuals with BCI equal to 1st and 3rd quartiles.

adult females were lactating at the time of sampling and had higher abomasal counts (median count = 22,400) than the other nine females (median count = 11,440) although with such a small sample size the difference was not significant ($\chi^2_{1,10} = 0.11$, p = 0.739).

4. Discussion

In this first study of abomasal parasite diversity and abundance in Norwegian moose, we found high nematode burdens compared with earlier studies and related host species (Nilsson, 1971; Nikander, 1989; Hrabok, 2006; Irvine et al., 2006; Santín-Durán et al., 2008; Hughes et al., 2009). *O. antipini* and *S. alcis*, which are specialist nematodes of wild cervids, were the most prevalent species and have previously been reported in moose in Scandinavia (Drózdz and Bylung, 1970; Nilsson, 1971; Nikander, 1989). However two other species, *O. leptospicularis*, and its minor morph *O. kolchida*, and *T. circumcincta* were also detected. These latter two are also known to infect domestic ruminants where they can cause significant morbidity (Torina et al., 2004; Domke et al., 2013). This is only the second report of *O. leptospicularis* in wild cervids in Norway, having previously been reported in red deer (Davidson et al., 2014). Our study did not show any significant relationships between parasite diversity and host age, sex or body condition.

Age and gender related trends were seen in nematode prevalence and intensity of infection. *O. antipini* was detected more frequently in yearlings and females than other age/gender classes, whilst burdens of *S. alcis* were significantly lower in adult males than other age/gender classes in this study. On the whole, female animals had higher mean abomasal nematode counts than males (although median levels were similar) and lactating females appeared to have higher counts than non-lactating females. But with just three lactating individuals sampled, these findings need further corroboration. The high energetic costs of pregnancy and lactation (Clutton-Brock et al., 1989), combined with the hormones involved during parturition and lactation, can have an immunosuppressive effect so increasing the susceptibility of females to parasitism during certain periods of the year (Dobson and Meagher, 1996). However, other factors such as gender related ecological differences in behaviour, diet and habitat choice can also impact parasite transmission (Wilson et al., 2002). Further work is needed to determine whether our findings apply to other moose populations.

As found earlier in red deer (Irvine et al., 2006), there was no strong evidence in this population for the development of acquired immunity to abomasal nematodes as prevalence and infection intensity increased with age. Calves and yearlings had a higher DSL infection probability than adults which could suggest young had lower acquired immunity to these nematodes than adults (Coop and Holmes, 1996). Two species of DSL (Protostrongylidae) are found in moose in Norway: *Elaphostrongylus alces* (Handeland and Gibbons, 2001) and *Varestrongylus alces* (Verocai et al., 2014). Measurement of the larvae was not carried out as part of our study so we were not able to morphologically distinguish which of these two species were present in the Hedmark population or whether mixed infections were also present. Further work on these species is needed. Animals with DSL larvae were in poorer condition than uninfected individuals. *Elaphostrongylus cervi* has been shown to negatively impact red deer body condition (Vicente et al., 2007). Stéen et al. (2005) reported elaphostrongylosis as the cause of mortality in 18% of moose in Sweden and also found that the disease was more prevalent in younger animals. *Varestrongylus* sp. are considered to be less pathogenic although recent work showed macroscopic focal lesions in the lungs and verminous pneumonia in moose in Norway (Verocai et al., 2014). Both species therefore have the potential to negatively influence growth and should be considered as having a potentially negative effect on moose health in young animals in particular.

We found similarly low levels of *Trichuris* infection to those of Milner et al. (2013b) during their study of moose in Hedmark. However, examination of moose submitted to Norwegian Veterinary Institute from other regions has revealed heavy *Trichuris* sp. burdens in emaciated individuals during winter (Norwegian Veterinary Institute, Oslo, unpublished data). None of our individuals were emaciated but there may also be seasonal or regional differences in *Trichuris* infection levels.

We found similar parasite species and prevalence among species identified by FEC to those of Milner et al. (2013b). However we also detected *Moniezia* sp., *Eimeria* sp. and *Strongyloides* sp. in our study which were not detected by Milner et al., possibly because the faeces in their study had been frozen prior to examination. A higher prevalence of *Nematodirus* sp. was detected by Milner et al. whilst the prevalence of *Trichuris* sp. was equally low. Age and gender related differences in faecal egg shedding were seen in our study. Faecal egg shedding depends on season (Houtert and Sykes, 1996), parasite fecundity (Stien et al., 2002) and host immunity, in addition to worm size and burden (Stear et al., 1995). Adult male moose had higher faecal egg counts than adult females despite having lower abomasal parasite burdens. This trend has also been reported in red deer although it was suggested that it was attributable to differences in harvesting season between the genders (Irvine et al., 2006). In our study, male and female moose were felled during the same time period so an alternative explanation could be reduced feed intake in rutting males, with a consequent reduction in faecal volume and concentration of eggs leading to apparent higher egg counts (Miquelle, 1990; Wilson et al., 2002). The faecal egg counts seen across our whole study population (calves, yearlings and adults) would suggest low levels of parasitism (median < 100 EPG) whereas the abomasal counts suggest the opposite, despite a significant positive correlation between female abomasal nematode counts and the FECs. Given that the majority of active surveillance work in wild cervids is carried out during the autumn hunting season any interpretation of faecal egg counts and related parasite pathogenicity should be guarded.

Over the last 20 years, moose carcass weights have been declining in some areas (Wam et al., 2010; Milner et al., 2012; Solberg et al., 2012). A decline in the relative availability of high quality forage is hypothesised as an important factor in this, with warmer summer temperatures leading to a general reduction in food quality and availability (Solberg et al., 2012) and changes in forestry causing a decrease in the area of successional forest (Milner et al., 2013a). Consequently moose carcass weights were shown to be higher in areas with low browsing pressure (Solberg et al., 2012). But our study suggests that nutritional availability may not be the only factor involved in the decline of moose carcass weights in areas of high population density. The negative correlation between body condition estimates and abomasal nematodes, as well as DSL and *Eimeria*, would suggest that parasites may also be playing a role. However, whether this is due to increased susceptibility to parasitism of individuals in poor condition, or poorer weight gain due to high levels of parasitism, or a combination of the two, is not possible to deduce from our study (see also Irvine et al., 2006). However, experimental studies in other wild ruminants, Soay sheep and Svalbard reindeer (*Rangifer tarandus*), as well as red grouse (*Lagopus lagopus*) have revealed that morbidity resulting from endoparasites can be substantial (Gulland, 1992; Hudson et al., 1992a, 1992b; Stien et al., 2002; Thomas et al., 2005). In these studies, high levels of parasitism were shown to reduce host body condition and reproductive success as well as increasing vulnerability to secondary causes of mortality such as predation and secondary infections. High population densities can lead to synergistic effects between parasite transmission dynamics and increased environmental contamination of free living stages of the parasites, as well as increased direct and indirect contacts between hosts (Body et al., 2011). Effects are compounded by increased competition for more limited nutritional resources which increase host susceptibility to parasite infections. Albon et al. (2002) found that reindeer host population density and parasite abundance were temporally linked, with a 2 year lag between high host population level and increased parasite abundance. Supplemental feeding, as is practiced in Hedmark, could further muddy the picture. Although no differences in faecal egg counts were found between moose using and not using supplemental feed (Milner et al., 2013b), abomasal counts might have revealed a different picture.

Health monitoring programs for wild cervids should include investigations of parasite status. Novel methods are required that can indicate to game managers whether parasites are an underlying problem and whether implemented countermeasures are having the required effect. As this study showed, faecal egg counts during the autumn hunting season may give a skewed picture and, as such, are not sufficiently reliable for estimating the impact of management decisions. However, the counting of abomasal parasites is labour intensive so unsuitable for widescale monitoring of parasite levels in large surveillance programs. Alternative methods for estimating endoparasite burden or endoparasite related damage are therefore required. Indirect measures of parasite burden are carried out in domestic animals using ELISA methods to measure antibody levels to specific parasites (Forbes et al., 2008; Höglund et al., 2010) and the measurement of serum pepsinogen (Charlier et al., 2011) to determine the degree of damage to the abomasal wall. Both methods could be promising areas for future research and adaptation for use in wild ruminants.

5. Conclusions

This study confirms that abomasal parasite intensities are high in moose in Hedmark. These high parasite burdens were associated with reduced body condition but independent of visually evaluated fat reserves. The most prevalent abomasal nematodes were *O. antipini* and *S. alcis*. Two other species complexes detected, *O. leptospicularis* and *T. circumcincta*, are both known to also infect domestic ruminants. Therefore farm parasite management strategies should take into account potential wildlife reservoirs in areas were grazing overlaps. Game managers should also be aware that field assessments of fat reserves are a coarse measure of body condition and together with autumn faecal egg counts are not sufficiently sensitive to reveal the impact of parasites on a population. The damage done by the endoparasites is more insidious, resulting in long term impacts on growth that may not be immediately visible at slaughter.

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Conflict of interest

The authors declared that there is no conflict of interest.

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