Low-level parasitic worm burdens may reduce body condition in free-ranging red deer (*Cervus elaphus*)

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SUMMARY

Regulation of ungulate populations by parasites relies on establishing a density-dependent relationship between infection and vital demographic rates which may act through the effect of parasites on body condition. We examine evidence for parasite impacts in 285 red deer (*Cervus elaphus*) harvested during 1991 and 1992 on the Isle of Rum. In the abomasa, prevalence of nematodes was 100% and the most abundant genus observed were *Ostertagia* species, however, mean intensity of infection was low (less than 1000) relative to other studies. Additional species, also present in low numbers, included *Nematodirus* spp., *Capillaria* spp., *Cooperia* spp., *Monieza expanza*, *Oesophagostomum venulosum* and *Trichuris ovis*. Lungworm (*Dictyocaulus* spp.) and tissue worm (*Elaphostronygylus cervi*) larvae were also observed in faecal samples. There was no evidence for acquired immunity to abomasal nematodes. Despite low levels of infection, both adult male and female deer showed significant negative correlation between indices of condition (kidney fat index, dressed carcass weight and larder weight) and intensity of *Ostertagia* spp. infection. However, there was no evidence that pregnancy rate in females was related to intensity of infection. For calves, there was no relationship between body condition and intensity of infection. The apparent subclinical effects of low-level parasite infection on red deer performance could alternatively be due to animals in poorer nutritional state being more susceptible to infection. Either way the results suggest that further studies of wild populations are justified, in particular where high local host densities exist or alternative ungulate hosts are present, and, where experimental treatments are tractable.

Key words: nematode parasites, red deer, cost of parasitism, body mass, body condition, pregnancy.

INTRODUCTION

Parasitic helminth infections cause production losses in domestic animals worldwide (Coyne and Smith, 1994). Rather than causing mortality, the effects are often subclinical, such as reduced appetite and food assimilation with consequences for growth, reproduction and lactation (Soulsby, 1982; Xiao and Gibbs, 1992; Arneberg *et al*. 1996; Fox, 1997; Forbes *et al*. 2000). For these reasons, most parasitological studies of ruminants have focussed on domestic animals but it is well established that parasitic helminth infections are just as common (Hoberg *et al*. 2001) and can have similar impacts on performance and fitness in wild animals (Gulland, 1995; Gunn and Irvine, 2003). Although these natural host-parasite relationships are typically more difficult to study, there are at least two reasons why they deserve closer inspection. First, theory predicts that these parasites may have a role in the regulation of animal populations (Anderson and May, 1978; May and Anderson, 1978). Although there is a paucity of examples, recent studies of wild Svalbard reindeer showed anthelmintic treatment increased body mass, back fat (a measure of condition) and pregnancy rates (Stien *et al*. 2002), and provided evidence that delayed density-dependent parasite-mediated changes in fecundity were sufficient to regulate the population (Albon *et al*. 2002). Second, environmental change, including climate change and land use change, particularly when causing habitat fragmentation, is perceived to increase the potential threat of parasites to natural populations (Harvell *et al*. 1999; Daszak *et al*. 2000).

In this study we explore the impact of helminth parasites on body mass, condition and pregnancy in red deer culled on the Island of Rum, off the west coast of Scotland. Despite red deer (*Cervus elaphus*) being one of the most widely distributed and better studied temperate wild mammals (Albon *et al*. 2000; Clutton-Brock *et al*. 1982; Coulson *et al*. 2001; Mysterud *et al*. 2002) the role of parasites in their population biology has not been investigated in any detail.

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MATERIALS AND METHODS

Study area

The data were collected on the Isle of Rum, Scotland (57°N 6°20′W) between August 1991 and February 1992 and from September to December 1992. The island has an oceanic, mild and wet, climate with little snow cover in most winters (Clutton-Brock and Ball, 1987). The habitat has been described in detail by Clutton-Brock and Ball (1987) as high quality herb-rich *Agrostis-Festuca*, a grassland heath and poorer quality *Trichophorum*, and *Molinia* heath. Rum is divided into 5 red deer management blocks according to natural geographical boundaries (Lowe, 1969). The density of deer in the summer of 1991 before culling was, on average, 13·9 deer per km^2 (S.D. = 0·021) (Clutton-Brock *et al.* 1997). The lack of competition from sheep and the absence of predation probably explains the relatively high density of red deer on the island. In 1991 a culling strategy was implemented to investigate the effects of female density on male numbers (Clutton-Brock *et al.* 2002) and carcasses from this cull formed the basis for parasitological sampling in this study. The cull took place with minimum disturbance using 3 experienced stalkers (professional hunters) employed by the Red Deer Commission (now the Deer Commission for Scotland) within the conventional hunting seasons (Clutton-Brock *et al.* 1997), Carcasses and samples were transported back to the larder and laboratory with the aid of up to 6 ghillies (stalkers' assistants) and ponies.

Assessment of physical condition and reproductive status

We used 3 indices of condition: larder weight, dressed carcass weight and kidney fat index. Body fat and weight follow pronounced seasonal cycles (Mitchell *et al.* 1976) and differences between individuals reflect demands of lactation and pregnancy. Albon *et al.* (1986) showed that body weight, kidney fat, and jaw length, another measure of skeletal size, all independently affected the probability of being pregnant.

Larder weight is the weight in kilograms of the whole animal (124 females, 76 males, 44 calves) less bleedable blood and the alimentary tract (Albon *et al.* 1983). Dressed carcass weight with skin (123 females, 60 males, 34 calves) was equivalent to larder carcass weight minus the head, feet, internal organs, fat, udder and genitals (Albon *et al.* 1983). Larder weight and dressed carcass weight are likely to be strongly correlated but we report an analysis of both and where possible, include a term for skeletal size using hind leg length. Hind leg length is only available for the 1991–92 season (87 females, 46 males). To determine the kidney fat index (KFI), the perinephric fatty tissue was removed from the abdominal cavity along with the kidneys, and the fat surrounding the kidneys removed. Then the KFI was calculated as kidney fat/kidney weight (106 females, 58 males, 34 calves; Suttie, 1983). Stalkers estimated the age of each individual by the degree of tooth eruption and wear (Lowe, 1967).

Animals that were not aged by tooth wear (Lowe, 1967) or sexed were excluded from the analysis. Those less than 1 year old were referred to as calves, those older than 1 but less than 2 were classed as yearlings and adults were any individual over the age of 2.

Reproductive status. Females were classified as either lactating or non-lactating on the basis of the presence of milk in the mammary gland. Pregnancy status was determined from 2 sources of information. Source 1 is based on the presence of a blastocyst or embryo in uterine flushings (Flint *et al.* 1997*a*, *b*). Most of this information came from early pregnancy (October to December). Source 2 came from the presence of a foetus in the uterus recorded in the larder where the carcasses were processed. This data spans from October to February.

Parasitological sampling

The intestines and abomasa were collected from 285 carcasses at the time of shooting. Cut ends of the small intestine and abomasa were closed using a cable tie and the material was placed in a bag labelled with the identity of the deer.

Within 24 h of death, the abomasums and the small and large intestine were opened and the contents washed out into separate buckets. The contents were diluted to 6 litres. A 300 ml (1/20th) homogenized aliquot was removed using a vacuum pump while the bucket was under constant agitation. These samples were stored in 10% formalin until they were counted. For counting the aliquot was washed over a 150 μm sieve, until no more food or matter would pass through. A larger 300 μm sieve was used for the large intestine. The whole of the aliquot was counted by inspecting small quantities in a Petri dish marked with tramlines under a dissecting microscope, at 16× objective magnification. The number of worms present in each aliquot was multiplied by 20 to determine the total number of worms in each gastrointestinal compartment. Each worm was identified to at least the genus level and in some cases to species.

An acid-pepsin digest of the abomasal mucosal lining was used to determine the number of immature larvae belonging to the Trichostrongylidae (MAFF/ADAS, 1986). The abomasum from each individual was chopped into small pieces and added to a jar containing 500 ml of this solution and incubated at 37 °C for 8–10 h. Subsequently, the mixture was washed over 2 mesh sieves (upper

75 μm, lower 38 μm). The retained trichostrongylid larvae were counted as above. Adult nematodes from the abomasums belonged to the subfamily *Ostertagiinae*. In the analysis these were added to the larvae extracted from the abomasal wall.

Faecal egg counts were determined using the modified McMaster technique (MAFF/ADAS, 1986). Eggs were categorized on the basis of morphological features into *Nematodirus* spp., *Trichostrongyle* spp. or *Trichuris ovis*. *Monieza expansa* were recorded as a presence or absence.

Larval output for *Dictyocaulus* spp. and *Elaphostrongylus cervus* were estimated using a faecal Baermann apparatus. Twenty-five g of faeces was suspended in water on a funnel and larvae were collected 24 h later by collecting the suspension from the tubing at the bottom of the apparatus. After centrifuging at 1000 rpm for 2 min the number of larvae was counted under ×40 power on a compound microscope by pipetting the spun down larvae onto a microscope slide and covering with a cover-slip (Hendriksen, 1965; MAFF/ADAS, 1986).

Statistical analysis

A feature of infection with abomasal nematodes is the high intensities in young, susceptible animals and the subsequent onset of immunity, which often produces lower levels of infection in older animals (Hudson and Dobson, 1995). However, inspection of the data seemed to indicate a much slower increase with age so that peak infection levels seemed to occur in 4 to 5-year-olds. We tested whether a model that allowed infection to increase with age to asymptotically and then decline in animals older than 5 years fitted the data. The main determinant of the increases in the intensity of infection with host age is thought to be the immigration-death process, which is fundamental in governing the growth of nematode infrapopulations. Assuming a constant net immigration rate (Λ) and per capita death rate (μ) of nematodes in the hosts, an age intensity curve will show a rise in parasite burden to an asymptote – the level of which is determined by the balance between infection and immunity (Anderson and May, 1978). The change in parasite abundance with time or host age can be described by the following differential equation:

$$\frac{dA(t)}{dt} = \Lambda - \mu A(t) \qquad (1)$$

where $A(t)$ is the abundance of infection at time t. If the host is uninfected at $t=0$ the solution to this differential equation is:

$$A(t) = A^{*}(1 - \exp(-\mu t)) \qquad (2)$$

where $A^{*} = \Lambda/\mu$ and gives the asymptotic equilibrium abundance of infection as:

$t \rightarrow \infty$.

The reciprocal of the mortality rate, $1/\mu$, can be interpreted as a crude estimate of the nematode's average life-expectancy and $A^{*} * \mu$ as a crude estimate of the average net transmission rate of parasites. The models were fitted using maximum likelihood. The likelihood ratio statistic was used to test for significant effects of the predictor variables and likelihood ratio based confidence intervals (C.I.) as measure of the precision of parameter estimates. The aggregated nature of the parasite data was taken into account in the age-intensity analysis by using a negative binomial error structure and allowing k, the aggregation factor, to increase with age (Pacala and Dobson, 1988).

The body condition of female red deer aged 2 years or older was analysed in relation to the abundance of abomasal nematodes using general linear models (SAS v8.1, SAS Institute Inc. USA). A separate analysis was carried out for males and females because they were culled in different time periods to coincide with the legal hunting season. Because of missing data for hind leg length, the analysis was initially carried out without accounting for this skeletal size. A second analysis using the subset where skeletal size was available was also conducted. Because adult females were culled from October to February, the seasonal decline in body condition due to the effects of winter was corrected by including a term for date in the models. Figures in the results show the relationship between the measures of body condition (which have been corrected for any seasonal trend) and parasite burdens.

Kidney fat index was not normally distributed and therefore was analysed in a generalised linear model using a Poisson error structure with a log link (Wilson *et al*. 1996; Wilson and Grenfell, 1997; SAS v8.1, SAS Institute Inc. USA). In this case, model fit is based on deviance values and F statistics.

The effect of parasite burden on pregnancy in adult females >2 years of age was analysed using a generalised linear model with and binomial error structure and logit link (SAS v8.1, SAS Institute Inc. USA). Because body mass and condition declines over winter in red deer (Clutton-Brock *et al*. 1982), models were corrected for dressed carcass weight and KFI (Albon, 1986). The source of the pregnancy information; either from blastocyst detection or from foetus detection, was fitted as a factor to take into account differences in these two methods. Worm burden was logged to take into account its skewed distribution.

RESULTS

Parasite species composition in the host

The most abundant helminth parasites in the gastrointestinal tract of adult Rum red deer were adults in the abomasum lumen belonging to the

Table 1. The mean parasite counts for a range of gastrointestinal parasites for adult male and female red deer categorized by location in the gastrointestinal tract

(Numbers in parentheses indicate the observed range and sample sizes are given at the top of each column.)

	Females					
	Non-pregnant		Pregnant			
Parasite (source)	Lactating $n=17$	Non-lactating $n=43$	Lactating $n=38$	Non-lactating $n=73$	Males $n=60$	Calves $n=35$
Adult nematodes (abomasum lumen)	718·6 (0–3600)	599·9 (0–2445)	684·2 (0–2750)	365·0 (0–2365)	200·7 (0–1620)	799·1 (0–4000)
Larval nematodes (abomasum mucosa)	8·4 (0–36)	10·4 (0–37)	10·9 (0–36)	7·2 (0–34)	2·2 (0–30)	4·9 (0–32)
Nematodirus spp. (small intestine)	23·2 (0–325)	2·7 (0–55)	1·7 (0–45)	2·1 (0–70)	12·3 (0–250)	3·8 (0–60)
Cooperia spp. (small intestine)	0 (0)	0 (0)	0 (0)	0·73 (0–25)	3·8 (0–90)	0·69 (0–20)
Capilaria spp. (small intestine)	0·71 (0–10)	0 (0)	0·19 (0–5)	0·18 (0–65)	4·2 (0–45)	3·6 (0–75)
Monezia spp. (small intestine)	0·07 (0–1)	0·08 (0–2)	0·19 (0–4)	0·02 (0–1)	0·3 (0–3)	0·24 (0–2)
Oesophagostomum venulosum (large intestine)	5·7 (0–25)	6·3 (0–40)	8·5 (0–30)	1·8 (0–20)	17·8 (0–95)	6·7 (0–35)
Trichuris spp. (large intestine)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Dictyocaulus larvae (faeces)	2·6 (0–22)	5·1 (0–118)	1·1 (0–16)	5·1 (301)	1·4 (0–25)	22·63 (0–263)
Elaphostrongylus cervi larvae (faeces)	79·0 (0–288)	95·9 (0–584)	73·1 (0–569)	97·2 (0–691)	26·3 (0–205)	108·1 (0–755)
Trichostrongyle spp. (faeces)	11·8 (0–100)	13·9 (0–150)	2·6 (0–50)	0·6 (0–50)	52·5 (0–10)	30 (0–150)

Ostertagiinae subfamily. Prevalence of this group was 100%. Females had the highest abundances (Table 1). Small numbers of larvae were also present in the abomasum mucosa. The small intestine was host to species of a number of different genera but abundances were low with the most common being *Nematodirus* spp. followed by *Cooperia* spp. and *Capillaria* spp. *Oesophagostomum venulosum* and *Trichuris ovis* were also present in low numbers in the large intestine. Small numbers of the cestode *Monieza expansa* were also recorded. Calf parasite assemblages were similar to that found in adults with a tendency to have higher levels of *Nematodirus* spp.

Faecal larval counts revealed low abundances of *Dictyocaulus* spp. larvae in adults but higher levels in calves. The abundance of larvae of the tissue-dwelling *Elaphostrongylus cervi* nematode were higher than the lungworm but similar between calves and adults (Table 1).

Faecal egg counts revealed low levels of *Trichostrongyle* spp. These cannot be directly correlated with worm burdens as they could not be identified to genus or species (Table 1). In addition to that reported in the table; 5 calves and 1 adult had *Nematodirus* spp. eggs; 11 adults were positive for *Capillaria* eggs. Seven adults and 1 calf had 50 coccidia oocysts per gramme of faeces.

Since abomasal nematodes were the most abundant parasites the remainder of the analysis focuses on this group.

The relationship between host age and intensity of infection

Fitting a non-linear immigration-death process function which allowed the intensity of infection to increase in early life and then decline with age did not provide a good fit to the data for either sex (Fig. 1). However, females had significantly higher worm burdens than males ($\chi^2=48{\cdot}8$, D.F.$=1$, $P<0{\cdot}01$). Allowing the aggregation term, k, to vary exponentially with the mean or to increase with age did not provide a better fit than a simple linear relationship between k and the mean ($\chi^2=1{\cdot}0$, D.F.$=1$, $P<0{\cdot}15$; $\chi^2=3{\cdot}0$, D.F.$=1$, $P>0{\cdot}08$ respectively).

Body condition and intensity of infection: adult females

Kidney Fat Index. There was a significant negative relationship between KFI and intensity of infection (Table 2A). However, the interaction between lactation status and intensity of infection indicates that the negative relationship only occurs in non-lactating animals (Table 2, Fig. 2A).

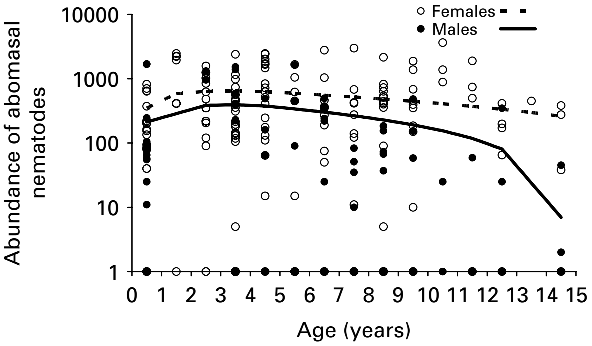

Fig. 1. Gompertz age – intensity curves for Abomasal ostertagid abundance sampled from male and female red deer on Rum. Observed values are plotted around the curves on the log scale. Red deer age is estimated by experienced stalkers. There was a tendency for younger and older animals to have lower worm burdens but there was no significant effect of age. Males had lower worm burdens than females.

Dressed carcass weight. There was a significant negative relationship between dressed carcass weight and intensity of infection (Table 2A). Again there was a significant interaction between lactation status and intensity of infection with the negative relationship only occurring in non-lactating animals (Fig. 2B). In an analysis of the subset of data where also we had a measure of skeletal size (hind leg length), there was still a significant negative relationship between dressed carcass weight and intensity of infection ($F_{1,79}=9{\cdot}58$, $P=0{\cdot}003$) although the interaction with lactational status was no longer significant ($F_{1,79}=2{\cdot}72$, $P>0{\cdot}1$).

Larder weight. There was no significant relationship between larder weight and intensity of infection after correcting for year, hunting block, the effect of pregnancy, lactation and the significant pregnancy∗lactation interaction (Table 2A).

However, in the subset of data where we have a measure of skeletal size (hind leg length), the best fit model demonstrated a significant negative relationship between larder weight and intensity of infection (Fig. 2C and Table 2A). In this case the rate of decline in larder weight within increasing worm burden did not differ between lactating and non-lactating, or between pregnant and non-pregnant animals.

Body condition and intensity of infection: adult males

All 3 measures of body condition: kidney fat index, dressed carcass weight, and larder weight, were negatively related to the intensity of infection (Fig. 2D–F). Larder weight and dressed carcass weight also varied significantly between hunting blocks but there was no significant interaction between block and intensity of infection (Table 2B).

Body condition and intensity of infection: calves

The body condition of calves ($n=44$) was not related to intensity of infection (Table 2c), nor were there any interactions with other explanatory variables.

Pregnancy and intensity of infection: adult females

After correcting for the source of pregnancy information source (see Materials and Methods section), sampling date, body mass and KFI, there was no significant relationship between pregnancy and intensity of infection (Table 3). There was no significant difference in pregnancy rates between lactating and non-lactating females. The significant effect of 'source' demonstrated that for the subset where pregnancy was based on uterine flushing methods ($n=83$) pregnancy was about 80% compared to 37·5% in the subset where pregnancy was based on the presence of a foetus ($n=28$). However, there were no significant interactions between pregnancy, intensity of infection and source, or any other of the factors considered in the models.

DISCUSSION

Our primary results are consistent with low intensity infections of abomasal nematodes depressing body condition in both adult female and male red deer on Rum. Interestingly, the apparent effects of these parasites occur despite being an order of magnitude less than other comparable studies of wild ruminants. For example, the highest level of infection with abomasal nematodes in our study was only 4000 (in an un-aged female) and the mean was less than 1000, compared to Soay sheep and Svalbard reindeer which would typically be around 10 000 adult abomasal nematodes (Gulland, 1992; Halvorsen *et al.* 1999; Wilson *et al.* 2004). The lower levels of body fat and lighter body weights in this wild herbivore are consistent with the effects found in domestic animal studies where reduced growth and poor condition is attributed to reduced food intake caused by inappetance and reduced food assimilation due to pathogenic effects of the nematodes on gut function (Fox, 1993, 1997; Arneberg *et al.* 1996; Forbes *et al.* 2000).

There is, however, an alternative explanation for the correlation between elevated parasite levels and poorer body condition. Animals with initial low fat reserves such as the lactating hinds may be more susceptible to infection, compared to non-lactating hinds. It is well established in domestic livestock that animals in poor condition are less likely to be able to

Table 2. ANOVA table for models of kidney fat index (KFI), dressed carcass weight (dwt) and larder weight (lwt) for (A) adult female red deer (B) adult male red deer and (C) red deer calves

(For the analysis of KFI, residual deviance, residual degrees of freedom (D.F.) and *P* values from χ^2 test are given. For dwt and lwt, residual sums of squares (RSS), D.F. and *P* values from F-tests are given. The significant terms are highlighted in bold. The statistics for the non-significant terms are from fitting them individually to the best model. Interactions (denoted by ∗) were tested after fitting the first order terms. In (A), the final 3 columns include an additional analysis of lwt where leg length was available (Ostertagid and Oster indicate abomasum nematode abundance.)

	KFI $n=106$			Dressed carcass wt $n=123$			Larder wt $n=124$			Larder wt (including leg length) $n=87$		
(A) Adult females	Deviance	D.F.	*P*	RSS	D.F.	*P*	RSS	D.F.	*P*	RSS	D.F.	*P*
Intercept	108·0			5006·9	122		7086·6	123		4684·2	86	
Time	**104·6**	**104**	**0·06**	**4694·3**	121	**0·005**	**6820·9**	122	**0·031**	**4420·1**	**85**	**0·027**
Leg length										**3604·8**	**84**	**<0·01**
Pregnancy	**63·4**	**103**	**<0·01**	**3669·8**	120	**<0·01**	**5122·7**	121	**<0·01**	**2605·0**	**83**	**<0·01**
Lactation	**48·5**	**102**	**<0·01**	3668·6	119	0·85	5095·3	120	0·42	2506·0	82	0·076
Preg. ∗ lact	**44·5**	**101**	**<0·01**	**3443·5**	118	**0·01**	**4627·7**	119	**<0·01**	**2191·1**	**81**	**0·01**
Ostertagid abundance	**40·8**	**100**	**<0·01**	**3286·8**	117	**0·02**	4525·5	118	0·11	**2052·8**	**80**	**0·01**
Oster. ∗ lact.	**38·5**	**99**	**0·013**	**3140·1**	116	**0·02**	4477·6	117	0·33	2051·5	79	0·82
Oster. ∗ preg.	38·4	98	0·85	3130·3	115	0·55	4489·3	117	0·26	2052·7	79	0·94
Cull year	38·2	98	0·42	3131·4	115	0·57	4627·3	117	0·27			
Block	37·6	98	0·13	3066·7	115	0·26	4595·9	117	0·67			

	KFI $n=58$			Dressed carcass wt $n=60$			Larder wt $n=60$		
(B) Adult males	Deviance	D.F.	*P*	RSS	D.F.	*P*	RSS	D.F.	*P*
Intercept	36·34	57		9421·7	59		15141·5	59	
Time	36·34	56	>0·98	9355·6	58	>0·5	15054·4	58	>0·5
Block	33·72	55	>0·11	**8503·5**	**57**	**0·054**	**13432·3**	**57**	**<0·01**
Ostertagid abundance	**25·91**	**56**	**<0·01**	**6820·9**	**56**	**<0·01**	**10411·4**	**56**	**<0·01**

	KFI $n=34$			Dressed carcass wt $n=34$			Larder wt $n=34$		
(C) Calves	Deviance	D.F.	*P*	RSS	D.F.	*P*	RSS	D.F.	*P*
Intercept	−34·30	33		409·58	33		533·05	33	
Time	−33·92	32	>0·53	390·97	32	>0·2	499·79	32	=0·15
Block	−33·88	31	>0·51	396·94	31	>0·6	513·01	31	>0·3
Ostertagid abundance	3·2342	32	>0·99	409·31	32	>0·8	532·88	32	>0·9

mount an immune response (Gershwin *et al.* 1985; Coop *et al.* 1995; Coop and Holmes, 1996; Coop and Kyriazakis, 2001; Houdjik *et al.* 2001) and are therefore susceptible to greater infection levels.

The relationship between host age and intensity of infection

Although worm burdens are relatively low in all the sampled animals there is no obvious decline in worm burdens with age or decrease in *k* (the negative binomial dispersion factor), which would indicate acquired immunity (Anderson and Crombie, 1984; Pacala and Dobson, 1988) indicating that evidence for acquired immunity is weak (Grenfell *et al.* 1995; Lloyd, 1995; Hudson and Dobson, 1995). The few studies that have investigated this in wild animals have found no clear evidence for this phenomenon (Irvine *et al.* 2000) and in some studies parasite burdens actually increase with age (Hudson and Dobson, 1995).

Sex differences in the intensity of infection

Males had significantly lower worm burdens than females. This sex difference is in contrast to that found in many other species (Moore and Wilson, 2002) and is probably due to the different seasons in which males and female adults are culled. The majority of males in this study were harvested in August and September. At this time of year they would be in the peak of condition, (Mitchell *et al.* 1976) and may be more resistant to parasite establishment. In contrast, females were harvested throughout the winter when their condition was in decline, which may account for the higher observed burdens.

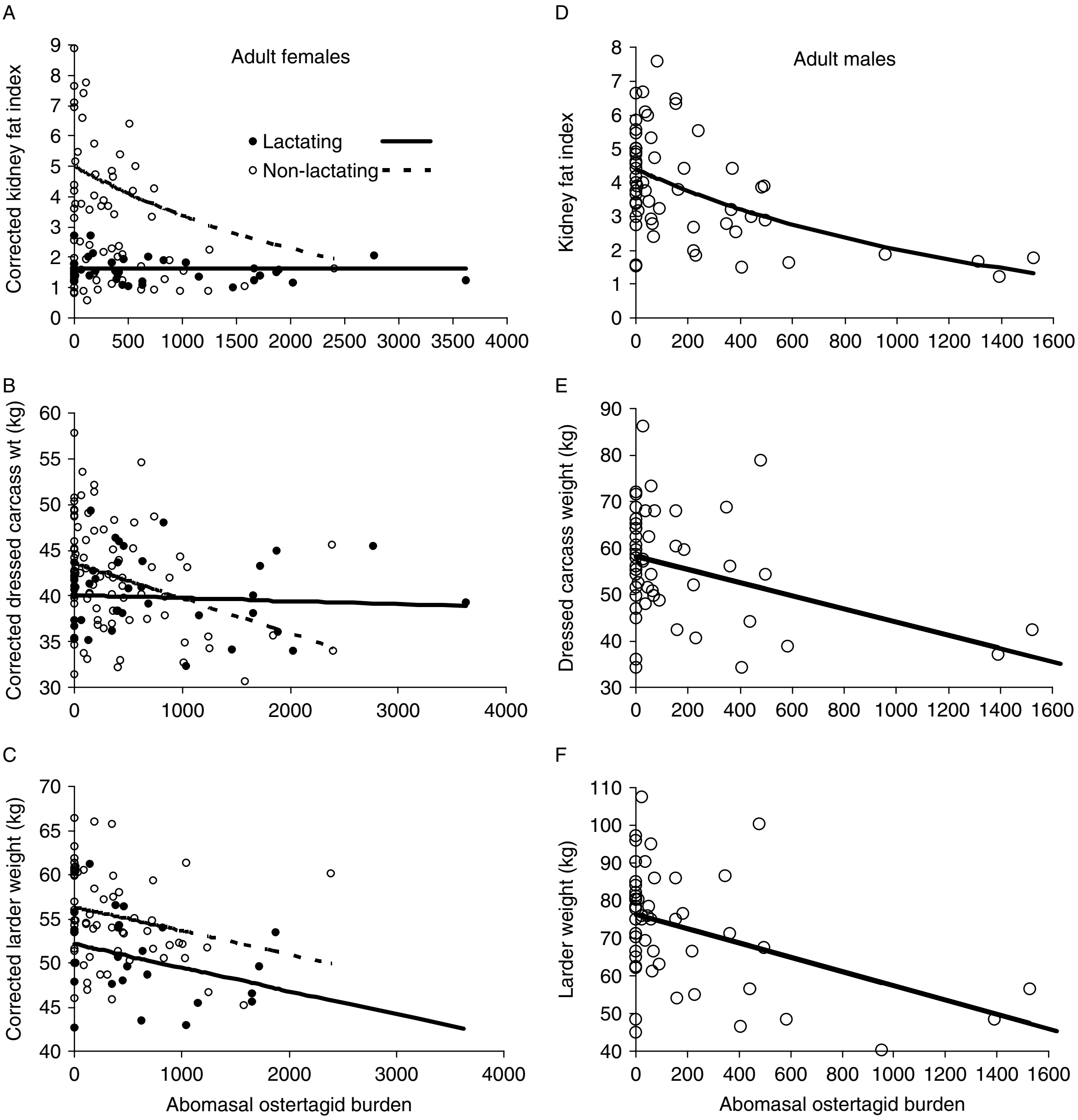

Fig. 2. (A) The negative relationship between kidney fat index (KFI) and the abundance of abomasal nematodes (adults and larvae) for non-lactating adult females (Yeld: estimated slope = exp (−0·0004), cl = −0·0007, −0·0002). There was no relationship for lactating adult females (Milk: estimated slope = exp (−0·0001), cl = −0·0000, −0·0002). The data and fitted line is corrected for the independent decline in KFI with time (estimate = exp (−0·0064) per day cl = −0·0088, −0·0039) and for the lower KFI found in pregnant animals (exp (−0·58), cl = −0·76, −0·40) for non-lactating adult females (Yeld: estimated slope = exp (−0·0004), cl = −0·0007, −0·0002). (B) The negative relationship between dressed carcass weight (kg) and the abundance of abomasal nematodes (adults and larvae) of non-lactating adult females (Yeld: estimated slope = −0·0038 ± −0·0012). There was no relationship in lactating animals (Milk: estimated slope = −0·0003 ± −0·0015). Milk animals were on average 3·4 kg (±1·51) lighter than Yeld animals. The data and fitted line are corrected for the independent decline in larder weight with time (estimate = −0·0623 ±0·0157) and corrected for weight differences due to pregnancy status. (C) The negative relationship between larder weight (kg) and the abundance of abomasal nematodes (adults and larvae) for adult females (estimated slope was −0·0027 ± −0·0011). This analysis uses the subset of data where skeletal size (leg length measures) was available. Lactating animals (Milk) were on average 4·13 kg (±1·53) lighter than non-lactating animals (Yeld). The data and fitted line are corrected for the independent decline in larder weight with date (estimate = −0·0638 ±0·0187), skeletal size (estimate = 0·3889 ±0·0737) and weight differences due to pregnancy status. (D) The negative relationship between kidney fat index (KFI) and the abundance of abomasal nematodes (adults and larvae) for adult males (estimated slope = exp (−0·0009), cl = −0·0013, −0·0005). There was no significant effect of time. (E) The negative relationship between larder weight (kg) and the abundance of abomasal nematodes (adults and larvae) for adult males (estimated slope = −0·0270 ± −0·0067). There was no significant effect of time. (F) The negative relationship between larder weight (kg) and the abundance of abomasal nematodes (adults and larvae) for adult males (estimated slope = −0·0197 ± −0·0053). There was no significant effect of time.

Table 3. ANOVA table for the analysis of pregnancy ($n = 105$) for adult female red deer (>1 year old). Deviance, D.F. and the *P* values from F-tests are given

(The significant terms are highlighted in bold. The statistics for the non-significant terms are from fitting them individually to the best model. Interactions (denoted by ∗) were tested after fitting the first order terms.)

	Pregnancy status $n = 110$		
	Deviance	D.F.	*P*
Intercept	139·6	104	
Source	**117·5**	**103**	**<0·001**
Date	**108·6**	**102**	**0·003**
Dressed carcass wt (kg)	**92·1**	**101**	**<0·001**
Kidney fat index	89·9	100	0·142
Lactation status	92·0	100	>0·83
Ostertagid abundance	89·3	100	0·098
Ostertagid abundance ∗ lactation.	88·4	98	0·32

during the rut. However, an experimental test of this relationship is needed to determine if the correlation is causal or whether stags that are in poor condition due to other causes may just be more susceptible to increased parasite loads due to a compromised immune response. One explanation lies in the theory that elevated testosterone associated with rutting or dominance is immunosuppressive and can result in increased parasitism (Folstad and Karter, 1992).

Contrary to the pattern in domestic animals where naïve calves can suffer more severe effects of parasitism (Parkins *et al.* 1990) there was no significant negative relationship between body condition indices and intensity of infection in calves. However, as the levels of infection seen in the majority of the calves were very low, negative impacts on condition were unlikely. This supports findings from reindeer calves in which there was no relationship between body mass and intensity of infection (Halvorsen and Bye, 1999).

The relationship between condition indices and intensity of infection

This study offers one of a few examples where the impacts of parasitism have been detected in cross-sectional studies (see Newey *et al.* 2005). Usually it requires experimental manipulation of the parasites or hosts in order to reduce the variance (Stien *et al.* 2002). The stronger relationship found for dressed carcass weight rather than larder weight with intensity of infection in hinds may be because the former is free of the variation in mass due to items such as skin, head and legs. Interestingly, when larder weight was analysed accounting for a measure of skeletal size (hind leg length), the results were much more comparable to the analysis of dressed carcass weight. The significant negative relationship between both KFI and dressed carcass weight and intensity of infection was only witnessed in non-lactating hinds and not in lactating hinds which tend to have depleted the kidney fat reserves (Mitchell *et al.* 1976; Moen, 1978). As hinds have to reach a threshold weight in order to conceive (Albon *et al.* 1986), the continual drain on resources induced by the parasite, would decrease the number of hinds capable of reproducing each year and may have implications for the dynamics of this population (May and Anderson, 1978). In this context, including more individual-based information such as lactation and pregnancy status in the analysis has important consequences for determining the impact of parasites on host population dynamics.

In adult males, the significant negative relationship between KFI, dressed carcass and larder weights and intensity of infection suggests that even in summer when animals are in prime condition, these relatively low worm burdens can depress body condition, which in turn may affect stag performance

The relationship between pregnancy and intensity of infection

We found no evidence for a significant relationship between the probability of pregnancy and intensity of infection in adult female red deer. Since the effect of abomasal parasites on reproduction in large ungulates tends to be small (Albon *et al.* 2002) testing for the negative effects of parasites in cross-sectional data can be difficult for both ecological and statistical reasons, because both small sample sizes and variation in age, body mass and condition can add to the variance (Stien *et al.* 2002). For example, body mass may be negatively related to intensity of infection but the individual intensity of infection may be a measure of fitness indicating that animals with higher levels of parasites may be better able to withstand parasite infestation and may therefore be fitter and more likely to become pregnant. Thus, both negative and positive relationships may be generated (Gulland, 1995). Furthermore, since, these parasites are food transmitted, fitter individuals may have more parasites because they have had greater access to food resources (Halvorsen and Bye, 1986; Halvorsen *et al.* 1999; Hutchings *et al.* 2000). However, as hinds have to reach a threshold weight in order to conceive, (Albon *et al.* 1986), the continual drain on resources induced by the parasite, would decrease the number of hinds capable of reproducing each year and may have implications for the dynamics of this population (May and Anderson, 1978). These confounding factors emphasize the need for controlled experimental tests of the impact of parasitism to support the more widespread cross-sectional work in this field.

These negative effects of relatively low levels of parasites support other studies that have investigated the effects of parasitic infections, which, rather than cause mass mortality, have more subtle effects on body condition (Gunn and Irvine, 2003) and pregnancy (Stien *et al.* 2002). These impacts are more likely to affect the population dynamics through relatively small reductions in the individual fitness accumulating as reduced population levels of survival and reproduction (Gaillard *et al.* 2000; Hudson *et al.* 1998; Albon *et al.* 2002; Newey and Thirgood, 2004) and through their interaction with nutrition and survival (Murray *et al.* 1997).

Levels of infection are often related to host density. For example, in wild reindeer, between-population parasite burdens are positively related to population density (Bye, 1987). While in reindeer on Svalbard annual changes in parasite burdens were correlated to host population density 2 years earlier (Albon *et al.* 2002) and the probability of pregnancy negatively related to worm burdens (Stien *et al.* 2002). On Rum, despite a mild wet climate that should favour the development and transmission of infective larvae, red deer density is comparatively modest (14 km^2) compared to other Scottish populations suggesting that parasite burdens, and hence their impact, may be higher in herds that exist at densities of up to 40 km^2 (Clutton-Brock and Albon, 1989).

There is some evidence for parasite transmission being influenced by the presence of multiple host species (Tompkins *et al.* 2000). On Rum, red deer are the only large herbivore and the absence of sheep (removed in 1957) may limit the risk of infection. The effect of parasitism is an increasingly pressing research topic as wild animal populations come into greater contact with livestock and compete for the same limited resources. In many cases co-existing wild and domestic herbivores share parasite species and the effect on parasite transmission to one host when the abundance of another competent host is changing needs further investigation. Potentially important examples include livestock grazing in wildlife reserves (Madhusudan, 2004) and in Scottish uplands where sheep and deer overlap (Clutton-Brock and Albon, 1989; Clutton-Brock *et al.* 2004).

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