RESEARCH ARTICLE

Little impact of over-winter parasitism on a free-ranging ungulate in the high Arctic

Anja Morven Carlsson[1,2,3] | Steve D. Albon[2] | Stephen J. Coulson[3] |
Erik Ropstad[4] | Audun Stien[5] | Kenneth Wilson[1] | Leif Egil Loe[6] |
Vebjørn Veiberg[7] | Robert Justin Irvine[2]

[1]Lancaster Environment Centre, Lancaster University, Lancaster, UK; [2]The James Hutton Institute, Aberdeen, UK; [3]Department of Arctic Biology, University Centre in Svalbard, Longyearbyen, Norway; [4]School of Veterinary Science, Norwegian University of Life Sciences, Oslo, Norway; [5]Norwegian Institute for Nature Research (NINA), Fram Centre, Tromsø, Norway; [6]Faculty of Environmental Sciences and Natural Resource Management (MINA), Norwegian University of Life Sciences, Ås, Norway and [7]Norwegian Institute for Nature Research (NINA), Trondheim, Norway

Correspondence
Robert Justin Irvine
Email: Justin.irvine@hutton.ac.uk

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Abstract

1. Macroparasites have a central place in wildlife ecology because they have the potential to regulate host populations through effects on reproduction and/or survival. However, there remains a paucity of studies that have demonstrated the regulatory role of these parasites in free-ranging animals.

2. Previous work on Svalbard reindeer demonstrated that the experimental removal of the parasitic gastrointestinal nematode *Ostertagia gruehneri* transmitted in summer, improved reindeer fecundity, and that the species was capable of mediating a density-dependent reduction in fecundity.

3. The main coexisting parasitic nematode in the system, *Marshallagia marshalli*, exhibits a contrasting life history with low abundances in summer and an increase during the winter. Here, we examine the impact of this over-winter infection on fitness of female reindeer in the same population.

4. Worm burdens were removed at the start of the winter in October using a novel delayed-release anthelmintic bolus. Body mass and pregnancy rates were recorded for animals recaptured five (February) and seven (April) months later. The sub-set of treated animals recaptured in February was treated again with anthelmintic to remove newly acquired nematodes. The experiment was replicated over six winters (2006/2007-2011/2012) with a total of 343 recaptures, comprising 145 individual animals.

5. We found little effect of anthelmintic treatment on reindeer body mass or pregnancy rates during the winter, suggesting that nematode infection during this time does not significantly affect fitness of Svalbard reindeer.

6. Our studies are consistent with marked virulence nutritional trade-offs in this system and highlights the need to integrate studies of parasite co-infection, interspecific competition and community ecology to understand parasite impacts on hosts.

1 | INTRODUCTION

Understanding the ecology of host–parasite systems in the wild has increasing relevance for two main reasons. First, parasites are integral components of ecosystems (Gómez & Nichols, 2013; Tompkins, Dunn, Smith, & Telfer, 2011) and can interact with ecological drivers in ways that may influence entire ecosystems (Hatcher, Dick, & Dunn, 2012; Thompson, Lymbery, & Smith, 2010). For example empirical and theoretical studies have demonstrated that parasites have the potential to regulate host populations through effects on reproduction and/or survival (Albon et al., 2002; Anderson & May, 1978; Dobson & Hudson, 1992; Hudson, Newborn, & Dobson, 1992; Irvine, 2006; May & Anderson, 1978). Second, the development and transmission of parasites is typically sensitive to environmental change, suggesting that their impacts will change in response to climate variation (Altizer et al., 2006; Brooks & Hoberg, 2007; Kutz et al., 2009; Smith, Acevedo-Whitehouse, & Pedersen, 2009; Thompson, Lymbery, Smith, et al., 2010).

Gastrointestinal nematodes are ubiquitous in nature and infect almost all wildlife species (Poulin, 2014). Although infection levels are usually sub-lethal, they can cause pathological (clinical and sub-clinical) changes in the gut which disrupt digestion, reduce appetite and impair nutrient uptake (Fox, 1997). Infections can, thus, have negative impacts on body condition, which is a key determinant of growth, fecundity and winter survival in many ungulates (Parker, Barboza, & Gillingham, 2009). To quantify the impact of parasites on host fitness, it is preferable to experimentally manipulate the parasite load (Irvine, 2006; Pedersen & Fenton, 2015). However, only a limited number of studies have successfully conducted these types of manipulations in wildlife (Ballesteros et al., 2012; Gulland, 1992; Hudson, Dobson, & Newborn, 1998; Murray, Keith, & Cary, 1998; Newey & Thirgood, 2004; Newey, Thirgood, & Hudson, 2004; Pedersen & Greives, 2008; Stien, Irvine, Ropstad, et al., 2002), mainly due to logistical and ethical challenges involved in such experimental studies in wild populations.

In the high Arctic (75°–81°N, 9–33°E), Svalbard reindeer (*Rangifer tarandus platyrhynchus*) provide a relatively simple system where there are no predators or competing large herbivores. The parasite community of the Svalbard reindeer is also simple, being dominated by two species of stongyle nematodes in the abomasum with contrasting life-histories: *Ostertagia gruehneri* and *Marshallagia marshalli* (Halvorsen & Bye, 1999; Irvine, 2001). Egg-output and transmission of *O. gruehneri* occurs mainly during the summer (Irvine, Stien, Halvorsen, Langvatn, & Albon, 2000; Stien, Irvine, Langvatn, et al., 2002), whereas *M. marshalli* egg-output is negligible in summer but peaks in winter (Irvine et al., 2001), when transmission also occurs (Carlsson, Irvine, et al., 2012). In addition reindeer exhibit marked seasonal difference in range and habitat use (Van der Wal et al., 2000). Thus, in winter, animals favour grazing on exposed ridges because snow is absent or thin on these areas. Eggs, deposited in faeces on this vegetation type do not develop in winter but rapidly develop to infective larvae as temperatures rise above zero during snowmelt. During the short 3 month snow free period, animals utilise the other vegetation communities returning to graze the ridge communities and to ingest the infective *M. marshalli* larvae. Therefore, in this system, it appears that infective larvae are more likely to be available on the vegetation the animals make most use of in winter (Carlsson, Irvine, et al., 2012). Previous experimental work on this host–parasite system, where animals were treated with an anthelmintic in April to reduce parasite burdens in summer, demonstrated that *O. gruehneri* reduce reindeer fecundity at high infection intensities (Stien, Irvine, Ropstad, et al., 2002), through its negative effect on host body condition (Stien, Irvine, Ropstad, et al., 2002). Furthermore, the study provided unique evidence for delayed density-dependent parasite-mediated changes in fecundity to play a role in the regulation of the host population (Albon et al., 2002). However, the experimental approach adopted in these studies targeted only the summer transmitting *O. gruehneri*, as the anthelmintic treatment only affected parasite infection levels and infection rates in the spring and summer. Because the abundance of *M. marshalli* in the reindeer population is negligible in summer and only increases to significant numbers during the winter (Carlsson, Irvine, et al., 2012; Halvorsen & Bye, 1999; Irvine et al., 2000) this species escaped the earlier experimental anthelmintic manipulation.

Although Svalbard reindeer develop large reserves of fat during the summer and autumn, these are not sufficient to meet their energy demands through the 8 months of winter (Tyler, 1986). Animals lose up to 50% of their body mass in challenging winters (Albon et al., 2017; Oritsland 1986; Tyler, 1987)—characterised by rain on snow and icing (Hansen, Aanes, Herfindal, Kohler, & Saether, 2011). This leads to poor over-winter survival and low calving rates the following summer (Albon et al., 2017; Hansen et al., 2013; Stien et al., 2012; Veiberg et al., 2017). Winter nutrition is therefore likely to be a particularly important factor determining reproductive success and survival (Albon et al., 2017; Ropstad, 2000). Nematodes are known to suppress food intake in reindeer (Arneberg, Folstad, & Karter, 1996), and the effect of parasitism on animal body condition has been shown to be accentuated when host nutritional status is compromised (Gulland, 1992; Jokela, Lively, Taskinen, & Peters, 1999; Jokela, Taskinen, Mutikainen, & Kopp, 2005; Murray, Cary, & Keith, 1997; Pedersen & Greives, 2008) depending on how nutrition is traded off between maintaining body mass and supporting an immune response (Garnier et al., 2017). Thus, the transmission and development of high abundances of *M. marshalli* occurs during a period when Svalbard reindeer are already under environmental stress. This suggests that this species, known to have an impact in

other systems (e.g. see Morgan, Shaikenov, Torgerson, Medley, & Milner-Gulland, 2005) could be expected to have a strong negative impact on Svalbard reindeer fitness. Here, we test this hypothesis by analysing data from an experiment that removed parasites from a subsample of individually marked Svalbard reindeer in six consecutive winters. We predicted that animals treated with anthelmintics, which removed nematodes over the winter, would have greater body mass and higher pregnancy rates in February and April, compared to non-treated, control, animals, and also, that the treatment effects would increase with winter severity.

2 | MATERIALS AND METHODS

2.1 | Experimental protocol

This study was undertaken in the Colesdalen-Semmeldalen-Reindalen valley system, Nordenskiöldland (77°50′–78°20′N, 15°00′–17°30′E), Svalbard from 2006 to 2012. Svalbard reindeer have been captured and marked in the study area since 1994, allowing capture, treatment and recapture of known age individuals (Albon et al., 2002; Stien, Irvine, Ropstad, et al., 2002). Each April from 2006 until 2011, all captured animals older than 12 months of age were randomly allocated to either the non-treated control group or the anthelmintic treatment group. In the latter group, the anthelmintic was administered via a novel delayed-release intra-ruminal bolus (Carlsson, Wilson, & Irvine, 2012) which acted to remove nematodes at the start of winter (October) providing protection against re-infection for around 4–5 weeks. After this period, animals became re-infected with the nematode *M. marshalli*, but not *O. gruehneri* which is only transmitted in the summer months (Carlsson, Irvine, et al., 2012; Carlsson, Wilson, et al., 2012). Animals receiving the delayed-release intra-ruminal bolus (DB) also received a single dose of short acting 1% moxidectin (Cydectin, Pfizer, UK) at 0.2 mg per kg live mass. This was to ensure that they were nematode free at the start of the experiment (Irvine, 2000) and that their acquisition of a new infection of *O. gruehneri* over the summer was standardised to the conditions pertaining to that experimental year. DB-treated animals that were recaptured 10 months after bolus administration (February the following year) were treated again, with a single dose of 1% moxidectin to remove any nematodes acquired since the effect of the DB had dissipated.

To determine the fitness consequences of nematode infection during winter on Svalbard reindeer, animals were recaptured 10 months (February) and again, 12 months (April) after administration of the DB. Not every animal in the treated and control group captured in April in any given year was recaptured 10 or 12 months later. An experimental period thus lasted 12 months, and was repeated over 6 years (2006–2012). In February 2012, it was not possible to capture reindeer due to extreme weather (icing) conditions, and we have no data from animals at this time-point. The time at which an individual was allocated to a treatment group is referred to as year$_{t-1}$ since the body mass and pregnancy measurements occur 10 and 12 months after this

allocation. In any given year, a captured animal could belong to one of four groups with respect to experimental treatment: Control Group 1: recaptured marked animals, but not treated in year$_{t-1}$; Treated Group 2: recaptured marked animals treated with the DB and injectable moxidectin in April of year$_{t-1}$; Treated Group 3: recaptured marked animals treated as in 2 but also treated with injectable moxidectin in February of year$_t$; or Group 4: Not caught in April year$_{t-1}$ and therefore not part of the experiment if captured in Feb or April year$_t$.

Once caught, reindeer were restrained by hand without using sedatives or medication (Milner et al., 2003). Live body mass was measured using a spring balance (100 × 0.5 kg; Salter Industries, West Bromwich, UK). Jugular venous blood samples were collected with evacuated heparinised tubes (Venoject®, Leuven, Belgium). Pregnancy status was determined by ultrasonography (Scanner 100, linear 3.5 MHz transducer, Pie Medical, The Netherlands) in the field via the bare skin of the udder, and verified subsequently using the progesterone concentration in blood samples (Ropstad et al., 1999). The foetus was recorded as live or dead depending on whether a heartbeat or body part movement was detected. All capture and live animal handling procedures were performed under licences from the Norwegian Animal Research Authority (FDU), with a veterinary surgeon in attendance.

The efficacy of the DB in reducing burdens of the different stages of *M. marshalli* and *O. gruehneri*, and the data and methods used to establish this are presented elsewhere (Carlsson, Irvine, et al., 2012; Carlsson, Wilson, et al., 2012). Here, we re-analyse these data to demonstrate the effect of treatment on total nematode abundance, i.e. the combined abundance of adult worms, lumen-dwelling larvae and mucosa-dwelling larvae. However, in addition to the sample used in the previous publications (*n* = 43, Carlsson, Irvine, et al., 2012), we have included data from a further four adult female reindeer that were culled in April 2009 to determine the efficacy of the additional moxidectin treatment administered in February (year$_t$).

2.2 | Statistical analysis

All analyses were performed using R version 3.3.2 (R Core Team, 2015).

2.2.1 | Effect of anthelmintic treatment on nematode abundance

The total nematode abundance in relation to treatment was analysed using a generalised linear mixed effects model (GLMM) with a negative binomial error distribution and a log link function (Wilson, Grenfell, & Shaw, 1996) using the function *glmmADMB* from the *glmmADMB* package (Pollitt, Reece, Mideo, Nussey, & Colegrave, 2012). For this part of the study, unmarked adult females (Group 4) were culled as controls (for details see Carlsson, Irvine, et al., 2012) as well as animals from Groups 2 and 3. Our assumption was that these unmarked adult females were from the same population as the marked females and that they would not be different with respect to infection

risk. This allowed us to maintain a maximum sample size in the marked control group for the study of treatment effects on body mass and pregnancy which relies on live recapture. Treatment was fitted as a 3-level factor categorised as either group 2, 3 or 4, as specified above. Month of culling was also fitted as a predictor variable to test for any temporal changes in parasite burdens over winter. Year was fitted as a random effect to account for random variation in annual worm abundances, where each winter sampled (i.e. 2006–2007) corresponded to one year.

2.2.2 | Effect of anthelmintic treatment on body mass and pregnancy

Over the six winters of the study there were a total of 343 recaptures of adult reindeer, comprising 145 individual animals. To test the effect of anthelmintic treatment on reindeer body mass and pregnancy we used data from animals caught in April of $year_{t-1}$, February and/or April the following year. Caught animals were categorised as yearlings if they were 12–24 months old and adults if they were older than 24 months of age in $year_{t-1}$. Due to a small number of recaptured yearlings ($n = 59$) and difficulties with respect to model convergence when these were included in the analysis, yearling and adult animals were analysed separately. For adult female reindeer, the effect of the anti-parasite treatment on body mass in winter (February and April) was analysed using linear mixed effects models (LMM) based on the *lme* function from the *lmer* package. The effect of treatment on pregnancy status in winter (February and April) was based on GLMMs using the *glmer* function from the *lme4* package with a logit link function assuming a binomial error distribution (Bolker et al., 2009). Based on work by Stien, Irvine, Langvatn, Albon and Halvorsen (2002), predictors included in the maximal models were Year (2007–2012), Month (February and/or April), Age and Age^2. Model simplification revealed that there was no significant difference in body mass ($F_{1,188} = 1.4$, $p = .24$) or pregnancy status ($\chi^2_{1,335} = 0.1$, $p = .70$) between Treated Groups 2 ($n = 110$) and 3 ($n = 36$) (as specified above), so these were collapsed into a single group. Treatment was therefore fitted as a two-level factor: non-treated animals (Group 1) and animals treated with the anthelmintic (Groups 2 and 3). Based on a priori expectations, interactions between Treatment and all other predictor variables were also fitted. Sample sizes for these analyses are presented in Table 1. To control for between-individual variation, reindeer identity was fitted as a random effect, however, in more complex models in the analysis of pregnancy these models did not converge. In these cases we ignored the within individual correlation and fitted standard logistic regression models. For yearlings, the effect of treatment on body mass was tested using ordinary linear regression. Predictor variables were as outlined above and only two-way interactions with treatment were tested in this analysis. Models were compared using likelihood-ratio tests and variables were retained in the model at $p < .05$. For model comparison, LMMs were fitted by maximum-likelihood and GLMMs were fitted by the Laplace approximation.

TABLE 1 Number of recaptures of female reindeer not-treated (Control) and treated with anthelmintic (Treated) in February and April 2007–2012. Over 6 years there were 343 recaptures, comprising 145 individual animals

Number of recaptured female adult reindeer				
	Control		Treated	
Year	February	April	February	April
2007	26	29	10	4
2008	21	18	9	10
2009	7	13	14	14
2010	22	22	17	22
2011	14	14	15	17
2012	0	11	0	14

3 | RESULTS

3.1 | Effect of anthelmintic treatment on nematode burden

Consistent with previous analyses (Carlsson, Irvine, et al., 2012), there was a significant effect of anthelmintic treatment on both the total nematode abundance and the abundance of each of the individual species (*O. gruehneri* and *M. marshalli*, $p < .0001$). Animals treated with the delayed-release bolus had significantly lower worm burdens than control animals throughout the winter (Figure 1). Animals that were also treated with an anthelmintic injection in February ended up with close to no (around 150) parasitic gastrointestinal nematodes in the subsequent April (Figure 1). There were no significant differences between sampling months ($p > .20$) or a significant interaction effect between treatment and sampling month ($p > .30$) on the total nematode abundance and the abundance of *O. gruehneri*. There was, however, some evidence for a significant treatment by month interaction effect on the abundance of *M. marshalli*, ($p = .05$). This was due to a greater rate of increase in abundance of *M. marshalli* in treated animals from a very low levels of less than 1,000 in October to around 6,600 in April, while over the same period the abundance of *M. Marshalli* in controls more than doubled from around 7,500 to 17,500 (Figure 1).

3.2 | Effects of winter parasitism on body mass and pregnancy

Animals were consistently heavier in February compared to April, with animals losing on average 18% of their body mass over the 2 months. There was also substantial inter-annual variation in body mass (Figure 2). However, there was no significant interaction between Year and Month, suggesting little between year variation in body mass loss between February and April (Table 2). There was no strong evidence for anthelmintic treated animals to be heavier than control animals (Table 2, Figure 2), and no evidence for a significant interaction between Treatment and other fixed effects (Table 2). The tendency was, however, for treated animals to be on average 0.6 kg ($SE = 0.5$) heavier than
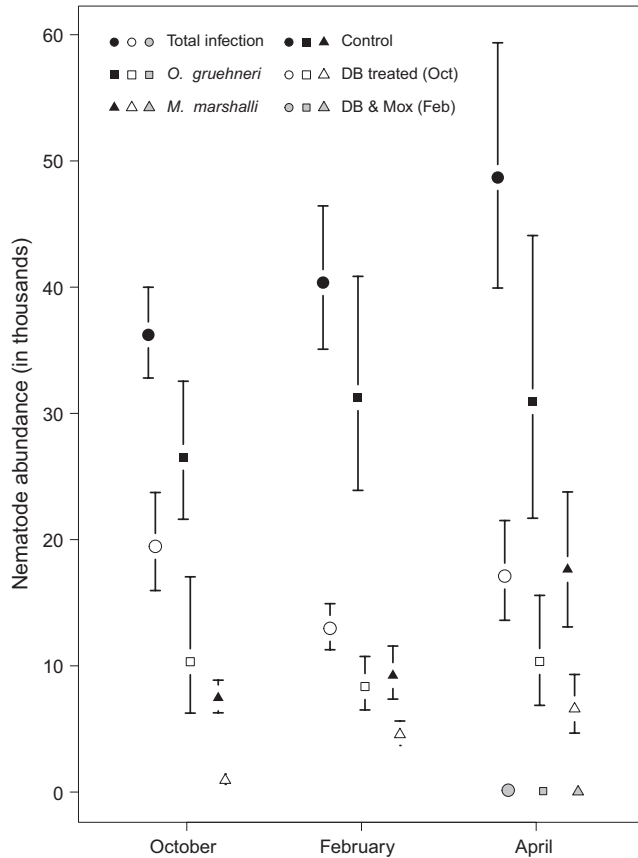
FIGURE 1 Nematode abundances (±1 *SE*, adult worms, lumen larvae and mucosa larvae combined) in adult female reindeer culled in October, February and April, 5, 10 and 12 months after administration of the delayed-release bolus. Circles gives the total nematode abundance (*Ostertagia gruehneri* and *Marshallagia marshalli* combined), whereas squares gives the abundance of *O. gruehneri* and triangles the abundance of *M. marshalli*. Black symbols represent animals in the control group, i.e. animals not treated with anthelmintic, open symbols represent animals treated with delayed-release intra-ruminal bolus in year$_{t-1}$ and grey symbols animals treated with both delayed-release intra-ruminal bolus in year$_{t-1}$ and injectable moxidectin in February year$_t$

control animals. In comparison, the estimated effect of anthelmintic treatment in the summer has previously been found to be significantly higher (1.9 kg, *SE* = 0.4, Stien, Irvine, Langvatn, et al., 2002; Stien, Irvine, Ropstad, et al., 2002) than this 0.6 kg estimate of effect size in winter.

Pregnancy rates for adult female reindeer showed marked inter-annual variation (Table 3, Figure 3). The average effect of anthelmintic treatment on pregnancy rates was not significantly different from zero (*p* = .26, Table 3), and the observed effect was not consistent across years (Figure 3). In some years point estimates of pregnancy rates were higher in the treated group when compared with the controls and in some years lower (Figure 3). Still, the overall trend was towards higher pregnancy rates in the treated group (Table 3), with on average 83% (*SE* = 10) of the control animals pregnant and 88% (*SE* = 8) of the treated animals.

There was no significant effect of Treatment on yearling body mass (*p* = .29), even though the trend was positive (effect size = 1.3 kg, *SE* = 1.2). There was no evidence for a significant interaction between
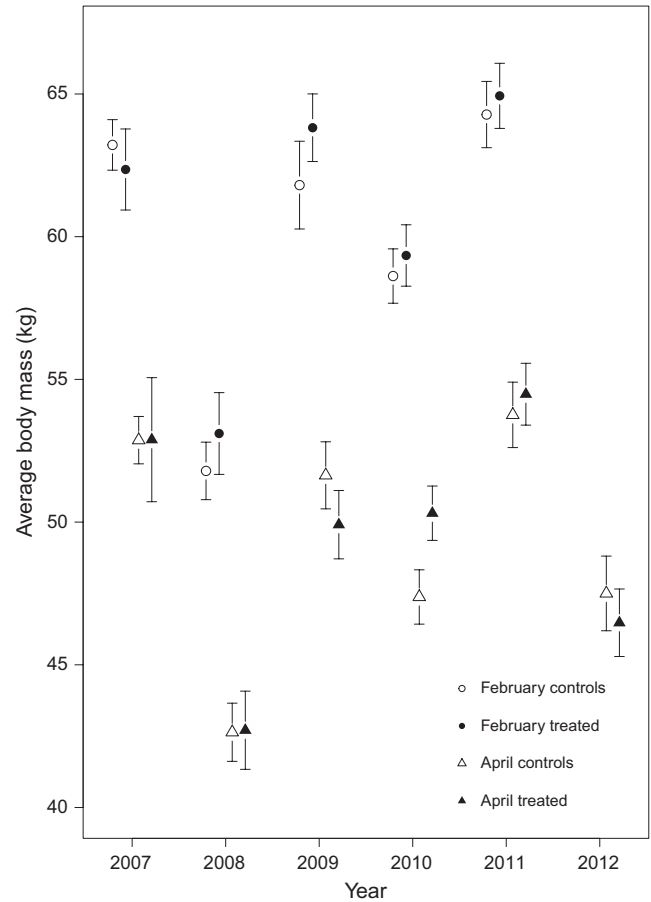

FIGURE 2 Mean annual body mass (±1 *SE*) for adult female reindeer. Estimates for non-treated controls (open symbols), animals treated with anthelmintic (filled symbols) in February (round symbols), and April (triangular symbols) after controlling for Age, Age[2] standardised to 6 year olds

Treatment and Month (*p* = .57) or Treatment and Year (*p* = .53) in models for average yearling body mass.

4 | DISCUSSION

Our longitudinal experimental manipulation of parasite burdens was effective in reducing the abundance of the winter transmitted *M. marshalli* in female reindeer but, to our surprise, we were not able to detect a significant effect of this treatment on host body mass or pregnancy rates.

The two main nematode species infecting Svalbard reindeer have contrasting life-history strategies, where reproduction and transmission occurs in winter for *M. marshalli*, and in summer for *O. gruehneri* (Carlsson, Irvine, et al., 2012; Irvine et al., 2000). Although fourth-stage larvae and adult worms of *O. gruehneri* remain at high levels in the host throughout the winter (Carlsson, Irvine, et al., 2012; Irvine, 2001), pathogenic effects are usually associated with the acquisition, maturation and reproduction of nematodes in the host (Fox, 1997). One would therefore expect any negative effects on host fitness during winter to mainly be due to *M. marshalli*, and not *O. gruehneri*. The

TABLE 2 Summary of the minimal linear mixed effects model predicting body mass of adult female reindeer, with reindeer identity fitted as a random effect. There was no effect of treatment on body mass. The estimated standard deviation of the random effect for between-individual variation was 2.93

Effect of treatment on body mass					
Term	Coeff.	SE	F-value	df	p
Intercept	51.76	2.27	26,417.5	1,190	<.001
Year					
2008	−10.48	0.76	64.6	5,190	<.001
2009	−1.05	0.82			
2010	−4.00	0.73			
2011	1.40	0.81			
2012	−5.74	1.06			
Month					
4	−10.41	0.44	561.7	1,190	<.001
Age	2.97	0.62	23.3	1,190	<.001
Age^2	−0.18	0.04	21.2	1,190	<.001
Excluded terms					
Treatment	0.62	0.50	1.54	1,189	.22
Treatment:year			0.74	5,184	.59
Treatment: month			0.25	1,188	.62
Treatment:age			2.21	1,188	.14
Treatment:age^2			0.09	1,187	.76
Month:year			0.91	4,186	.46
Treatment: month:year			0.83	4,175	.60

TABLE 3 Parameter estimates for the minimal generalised linear mixed effects model predicting pregnancy rates of adult female reindeer, and likelihood-ratio test statistics for an extended set of models. The models were fitted assuming a binomial error structure, a logit link function. Reindeer identity fitted as a random effect in the simpler model, while ordinary generalised linear models were fitted to the more complex models (*) due to convergence problems. The estimated standard deviation of the random effect for between-individual variation was 2.05 in the model including only year as fixed factor

Effect of treatment on pregnancy					
Term	Coeff.	SE	χ^2	df	p
Intercept	5.1	1.1			
Year					
2008	−6.3	1.1	94.4	5	<.001
2009	−2.7	1.2			
2010	−2.1	1.0			
2011	−2.9	1.0			
2012	−4.1	1.1			
Excluded term					
Treatment	0.51	0.46	1.3	1	.26
Month			1.6	1	.21
Age			0.2	1	.63
Age^2			0.2	1	.65
Treatment:year*			8.8	6	.18
Treatment:month*			2.2	3	.53
Treatment:age*			2.5	3	.47
Treatment:age^2*			2.6	3	.46
Month:year*			5.9	5	.32
Treatment:month:year*			17.2	16	.37

lack of an effect is in contrast with other studies in caribou (*Rangifer tarandus groenlandicus*) (Steele et al., 2013), Saiga antelope (*Saiga tatarica*) (Morgan et al., 2005), Dalls sheep (*Ovis dalli*) (Aleuy, Rucksthul, Hoberg, Veitch, & Kutz, 2016) and domesticated sheep (Igrashev, 1973), which have found negative correlations between *M. marshalli* infection and body condition. Whilst, previous experimental work on Svalbard reindeer has revealed a significant effect of *O. gruehneri* removal over the summer on both body mass and pregnancy rates (Stien, Irvine, Ropstad, et al., 2002) with implications for the host population regulation (Albon et al., 2002), and similar effects have been found in other studies of natural host–parasite systems (Bedhomme, Agnew, Sidobre, & Michalakis, 2004; Coop & Kyriazakis, 2001; Ferguson & Read, 2002; Gulland, 1992; Jokela et al., 1999; Krist, Jokela, Wiehn, & Lively, 2004; Murray et al., 1997; Pedersen & Greives, 2008; Restif & Kaltz, 2006), there is little evidence that *M. marshalli* has an impact on Svalbard reindeer fitness.

Many studies of host–parasite relationships in the wild suffer from not being able to detect an effect of parasites, due to difficulties in inferring relationships from cross-sectional data or small sample sizes (Gulland, 1995; Stien, Irvine, Ropstad, et al., 2002). However, we managed to perform a long-term experimental study with relatively large sample sizes in an environment with few confounding factors and where

individual and between-year variation in body mass and pregnancy status could be controlled for. We should, therefore, have been able to tease apart any effects of parasitism on body condition from other confounding factors, as has been achieved previously (Albon et al., 2002; Stien, Irvine, Ropstad, et al., 2002). As such, it was surprising that removing *M. marshalli* from Svalbard reindeer did not have any clear beneficial effect on adult or yearling body mass. There are at least three explanations to why we did not detect an effect of *M. marshalli* on fitness.

First, the small effect size of the anthelmintic treatment on host fitness in this study may be due to the timing of fitness measurements. Individual body condition of ruminants varies cyclically with seasonal changes, which has been attributed to changes in resource quality and availability, as well as energy and protein requirements (Parker et al., 2009). For northern ungulates, particularly in the Arctic, food is abundant only during the short summer season, and during winter, snow and ice limits access to food, and increases energetic demands. In our study system individuals caught in February, and again in April, persistently show a decline in body mass (Albon et al., 2017) indicating that they are under nutritional stress which could be expected to interact with parasite virulence. We therefore expected to be able to
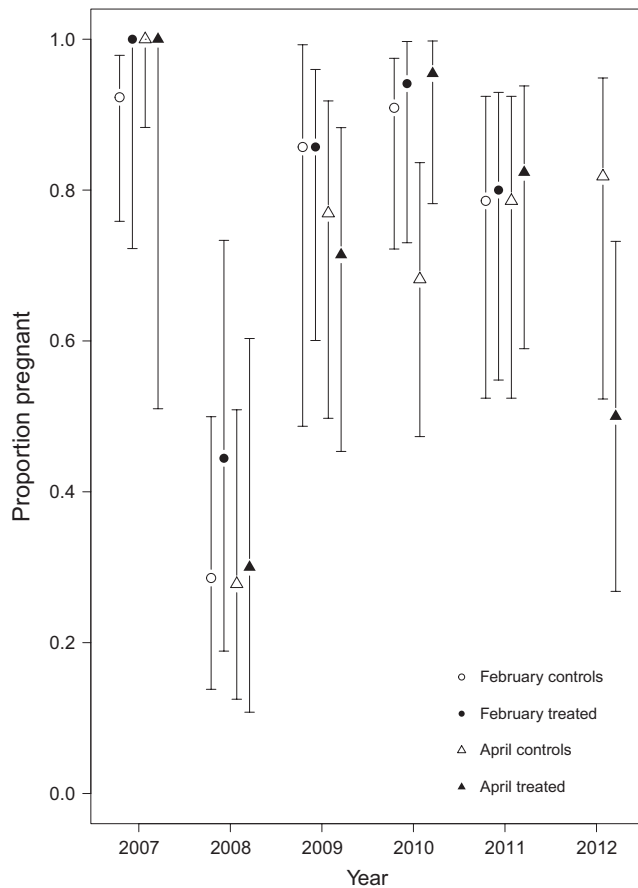
FIGURE 3 Mean annual pregnancy rates (±95% CI) for adult female reindeer. The estimates are for non-treated, controls (open symbols), animals treated with anthelmintic (filled symbols) in February (round symbols) and April (triangular symbols)

detect the impact of parasite removal on host fitness measured during the winter when animals are at their most vulnerable. However, previous studies have found that female northern ungulates are in their poorest condition in spring/early summer—2–3 weeks *after* parturition—in spite of increasing food availability and reduced snow cover at this time (Cameron, Smith, Fancy, Gerhart, & White, 1993; Chan-McLeod, White, & Holleman, 1994). This can in part be attributed to the high energetic demands of late pregnancy and lactation, as well as the depleted levels of fat reserves (reviewed in Parker et al., 2009). This study measured body mass 6–8 weeks *before* parturition. Effects of the anthelmintic treatment in this study may have been observed if body mass was measured post-calving in late June/early July—a time of year when this is not logistically feasible on Svalbard.

A second explanation could be that the effect of summer parasite removal may be acting through the constraints on energy and nutrient assimilation during the season when animals need to increase body condition to breed again and survive the subsequent winter. As reviewed by Parker et al. (2009), the yearly energy balance for northern ungulates is more sensitive to variation in energy intake than energy costs, because energy intake during summer and autumn largely determines body mass and body fat levels. Female ungulates are typically in best condition at the beginning of winter, and the fat and body mass

accumulated during the summer and late autumn can buffer the effect of declining food supplies when energetic demands cannot be met by foraging alone (Parker, Gillingham, Hanley, & Robbins, 1999) and allow the animals to withstand the impact of *M. marshalli* as its transmission picks up with the onset of winter. In support of this, studies on the factors affecting pregnancy have shown that for some northern ungulates the probability of carrying a foetus to term is determined primarily by the previous summer's weather conditions and autumn body mass (Cameron et al., 1993; Cook et al., 2004; Crete & Huot, 1993). However, on Svalbard winter body mass better explains pregnancy rates in April and the proportion of calves at heel in July/August with no apparent residual effects of the previous summer (Albon et al., 2017; Veiberg et al., 2017). Linked to the nutritional status of an individual is the immune response that, as a means to control infections, is subject to trade-offs between the partition of nutrition towards immunity and other metabolic needs (Garnier et al., 2017). Previous work on our study system demonstrates that there is no evidence for acquired immunity with adults maintaining high levels of abundance throughout the age range (Irvine et al., 2000). Thus, adult female Svalbard reindeer in winter may be conserving protein for survival rather than mounting an immune response. Whilst it is possible that our sample of control animals was biased if individuals most affected by *M. marshalli* died and therefore were not re-sampled, female adult mortality in this system is generally very low. Nonetheless, it can rise to around 15% in winters when rainfall occurs and refreezes, excluding animals from the vegetation, and causing starvation particularly in years when the reindeer density is high (Peeters et al., 2017). However, there is little evidence for a relationship between *M. marshalli* abundance and reindeer density (Carlsson, Irvine, et al., 2012; Irvine et al., 2000).

A third interpretation of our results is that the virulence of the gastrointestinal parasites during winter is in fact too low to cause a demonstrable impact on condition and pregnancy in this study system. There is evidence indicating that interactions between co-infecting parasite species, life-history strategies and host characteristics can impact on parasite virulence (Alizon, de Roode, & Michalakis, 2013; Rigaud, Perrot-Minnot, & Brown, 2010). In general, theory suggests that if hosts differ in quality, parasites are expected to evolve towards optimal virulence depending on the context; with higher transmission (and hence virulence) in higher quality hosts (as measured by parasite reproductive potential within a host, parasite prevalence within the host species and host abundance) (reviewed in Rigaud et al., 2010). As such, it is plausible that *M. marshalli* has evolved low virulence due to it infecting Svalbard reindeer during the winter, when they are in poor condition and mortality is relatively high. Furthermore, most theories for the evolution of parasite virulence assume that parasites tend to maximise the number offspring produced to increase transmission rate and, as such, fitness. But, increased replication rates leads to increased virulence (i.e. parasite-mediated reduction in host fitness), which reduces the duration of infection and chance of transmission (due to host mortality/decreased host density). Thus, a trade-off model predicts a positive correlation between the level of virulence and the reproductive fitness of the parasite (Bull, 1994). Consistent with these predictions, *M. marshalli* has a lower rate of production of transmission

stages (8 eggs/gram in April) compared to *O. gruehneri* (235 eggs/gram in July), during peak transmission times (Irvine et al., 2000). And, as this study demonstrated *M. marshalli* has little impact on the host, whereas *O. gruehneri* has a significant, negative impact on body condition and fecundity (Albon et al., 2002; Stien, Irvine, Langvatn, et al., 2002). This suggests that the virulence of the gastrointestinal parasites of Svalbard reindeer may be higher during the summer when transmission coincides with times when food availability is good, and low in winter when transmission coincides with times when environmental conditions are poor and the animals are starving.

The parasite community structure might also explain the observed virulence. The nature of co-infections can have consequences for future infection risk (Telfer et al., 2010) and for host fitness (Beechler et al., 2015; Johnson & Hoverman, 2012; Woolhouse et al., 2015). In the Colesdalen-Semmeldalen-Reindalen valley system on Svalbard, where this study was conducted, *O. gruehneri* is the numerically dominant parasite (Carlsson, Irvine, et al., 2012; Irvine et al., 2000). On the other hand, in systems with wild-free-ranging hosts where infection with *M. marshalli* has been correlated with negative impacts on body condition and/or pregnancy, *M. marshalli* is the most prevalent and numerically dominant parasite (Saiga antelope: Morgan et al., 2005; Dalls sheep: Aleuy et al., 2016 and caribou: Steele et al., 2013). Furthermore, in Dalls sheep, transmission of *M. marshalli* occurs year round, thus maintaining pressure on the host throughout the year (Aleuy et al., 2016), whilst transmission is restricted to the winter months on Svalbard (Carlsson, Irvine, et al., 2012). However, there are other theoretical models that suggest selection for reduced or increased virulence, depending on the nature of in-host–parasite interactions (Altizer, Ostfeld, Johnson, Kutz, & Harvell 2013; Staves & Knell, 2010). Since this study was not designed to investigate these questions, further carefully constructed experiments would have to be conducted to confirm the mechanisms at work in this system.

Finally, it is important to recognise that the taxonomy and systematics of *Marshallagia* across its reported range has not been well defined (Drozdz, 1965, 1995; Hoberg, Abrams, Pilitt, & Jenkins, 2012) and it may, in fact, consist of a species complex. One could therefore speculate that the genospecies of *M. marshalli* on Svalbard is distinct from others and is relatively benign.

5 | CONCLUSION

Our findings demonstrate that in systems where there are co-infections with two broadly similar trichostrongyles, one can have a regulatory effect on the population dynamics of the host, whereas the other may have no detectable effect despite focussing its transmission in winter when animals would be expected to be more susceptible to the impact of parasites. The results from our experiment indicate that over-winter infection with *M. marshalli* is of minor importance in regulating reindeer populations, possibly because it has evolved low virulence to limit its impact during its transmission window which occurs when the hosts undergo the nutritional stress of the Arctic winter. Other similar experiments with anthelmintics on natural populations of snowshoe

hares also produced only minimal effects on reproduction and survival (reviewed in Krebs, Boonstra, Boutin, & Sinclair, 2001). In that case, it was concluded that, although parasites may have indirect effects and sporadically affect hare populations, they are not essential for causing the observed population cycle.

Our results demonstrate that taking account of the parasite community ecology and infection dynamics is critical to understanding host impacts. It highlights the importance of considering the interplay between different ecological factors and life-history traits of hosts and parasites when determining the role of parasites in population dynamics. It is rare to be able to measure the impact of one of the parasite species in a mixed infection and as this study demonstrates. Thus the complexity of the impact of a community of parasites on the host needs to be considered but this is rarely discussed in experimental studies of natural host–parasite systems.

AUTHORS' CONTRIBUTIONS

S.D.A. and R.J.I. formulated the idea. A.M.C., R.J.I. and S.D.A. designed the experiments. All authors were involved in conducting the fieldwork and experimental treatments. A.M.C., S.D.A. and A.S. performed the statistical analysis of the data. A.M.C. wrote the manuscript; other authors provided editorial advice.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.j327n (Carlsson et al., 2018).

ETHICAL APPROVAL

All applicable institutional and/or national guidelines for the care and use of animals were followed.

ORCID

Robert Justin Irvine http://orcid.org/0000-0002-0411-6217

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