

The role of parasites in the dynamics of a reindeer population

S. D. Albon^{1*}, A. Stien^{1,2}, R. J. Irvine^{1,3}, R. Langvatn^{2,4}, E. Ropstad⁵ and O. Halvorsen⁶

¹Centre for Ecology and Hydrology, Hill of Brathens, Banchory AB31 4BW, UK

²University Courses on Svalbard (UNIS), Longyearbyen, N-9170, Norway

³Department of Biological and Molecular Sciences, University of Stirling, Stirling FK9 4LA, UK

⁴Norwegian Institute for Nature Research (NINA), Tunasletta-2, Trondheim, N-7040, Norway

⁵Norwegian College of Veterinary Medicine, Ullevålsveien 72, PO Box 8146, N-0033 Oslo, Norway

⁶University of Oslo, Zoological Museum, Sarsgate 1, N-0562 Oslo, Norway

Even though theoretical models show that parasites may regulate host population densities, few empirical studies have given support to this hypothesis. We present experimental and observational evidence for a host–parasite interaction where the parasite has sufficient impact on host population dynamics for regulation to occur. During a six year study of the Svalbard reindeer and its parasitic gastrointestinal nematode *Ostertagia gruehneri* we found that anthelmintic treatment in April–May increased the probability of a reindeer having a calf in the next year, compared with untreated controls. However, treatment did not influence the over-winter survival of the reindeer. The annual variation in the degree to which parasites depressed fecundity was positively related to the abundance of *O. gruehneri* infection the previous October, which in turn was related to host density two years earlier. In addition to the treatment effect, there was a strong negative effect of winter precipitation on the probability of female reindeer having a calf. A simple matrix model was parameterized using estimates from our experimental and observational data. This model shows that the parasite-mediated effect on fecundity was sufficient to regulate reindeer densities around observed host densities.

Keywords: *Rangifer tarandus*; nematodes; *Ostertagia*; calving rates

1. INTRODUCTION

Theoretical models suggest that parasites can have regulatory effects on the population dynamics of hosts (Anderson & May 1978; May & Anderson 1978). However, even though an increasing number of wildlife studies suggest that parasites sometimes depress host reproduction and/or survival (Gulland 1995) there are still surprisingly few that give empirical support to this hypothesis. Among host–macroparasite systems, the study of *Trichostrongylus tenuis* infections of red grouse (*Lagopus lagopus scoticus*) in northern England (Hudson *et al.* 1985, 1992, 1998; Hudson 1986; Hudson & Dobson 1995) is one exception. In this system, the caecal worms can drive host population cycles as a result of their low level of aggregation, and the time delay in their impact on the fecundity of grouse (Dobson & Hudson 1992).

The paucity of examples of the dynamical consequences of macroparasites on their hosts may reflect both (i) the difficulties inherent in teasing out the effect of parasites in complex ecological systems with many potentially confounding factors; and the fact (ii) that it is difficult to obtain funding for long-term studies of multispecies systems. The Svalbard reindeer (*Rangifer tarandus plathyrinchus*) with their gastrointestinal nematodes is a comparatively simple, wild, large mammal system in which to study host–parasite interactions. In the high

Arctic habitat on Svalbard, there are no mammalian herbivores competing for forage (no musk ox, *Ovibos moschatus*) or mammalian predators (no wolves, *Canis lupus*). Also, the parasite community of the Svalbard reindeer is very simple, dominated by only two species of strongyle nematodes in the abomasum, *Ostertagia gruehneri* and *Marshallagia marshalli* (Bye & Halvorsen 1983; Halvorsen & Bye 1986, 1999; Dallas *et al.* 2000; Irvine *et al.* 2000). These parasitic nematodes have a direct life cycle with no alternative hosts available on Svalbard. Of these, only *O. gruehneri* appears to be pathogenic, since high intensities of *O. gruehneri*, and not *M. marshalli*, infection are associated with reduced reindeer pregnancy rates (Stien *et al.* 2002).

Previous studies have shown that local reindeer population densities fluctuate over a twofold range, and that the apparent birth and death rates covary (Tyler & Øritsland 1999). A significant part of these fluctuations has been attributed to stochastic weather events, where winters with high precipitation are characterized by poor survival and low birth rate in the subsequent summer (Reimers 1982; Solberg *et al.* 2001), and hence low or negative population growth (Aanes *et al.* 2000). Changes in birth rate may be the ‘key factor’ limiting numbers (Tyler 1987), and it has been suggested that the birth rate shows over-compensatory density-dependence in two sub-populations: Adventdalen (Tyler & Øritsland 1999) and Colesdalen–Reindalen (Solberg *et al.* 2001).

We describe the results of an anthelmintic treatment experiment conducted over six years, which enabled us to

* Author for correspondence (s.albon@ceh.ac.uk).

separate out the stochastic effects of winter weather, and to measure the density-dependent parasite-mediated effects on the fecundity and survival of reindeer. In addition, the abomasa from reindeer shot each October enabled us to quantify the temporal relationship between parasite abundances and host densities. Finally, we used this information to parameterize a model of the role of parasites in the regulation of the reindeer population.

2. MATERIAL AND METHODS

(a) *Study area and reindeer population*

The study was undertaken in Nordenskiöldland, Spitsbergen (77°50'–78°20' N, 15°00'–17°30' E). Female reindeer were caught and marked in the Colesdalen–Semmaldalen–Reindalen valley system in August 1994 and from 1995 in late April/early May each year. Individual reproduction and survival were monitored by census in the summer and recapture in subsequent winters. The experimental manipulation of parasite burdens was undertaken by anthelmintic treatment (see below). Estimates of the annual abundance of gastrointestinal nematodes came from the abomasa of reindeer older than one year and culled in October. Approximately 40% ($n = 45$) of the reindeer were sampled in Colesdalen to limit the impact on population size, and the remainder ($n = 66$) from Sassendalen, a valley ca. 50 km east of Colesdalen. Reindeer densities have been estimated from summer helicopter counts in Colesdalen (145 km²) since 1992 and Sassendalen (398 km²) since 1993, conducted by the Environmental Department of the Governor of Svalbard's Office. The meteorological data used in the analysis were collected at Longyearbyen airport (78°15' N, 15°28' E) and Svea (77°54' N, 16°48' E) by the Norwegian Meteorological Institute. Our study area lies between these two stations and we used the means of the values from the two stations for the analyses.

The climate is severe. Mean daily temperature in January is –16 °C and in July +6 °C. Annual mean precipitation is only 200 mm with most falling as snow in winter and persisting from October to early June. Thus, the growing season for plants is short and productivity low, typically 40–60 g m⁻² (Wegener & Odasz-Albrigtsen 1998). Although Svalbard reindeer do not undertake seasonal migrations, local emigration does take place in severe winter weather (Tyler 1987; Tyler & Øritsland 1989; Aanes *et al.* 2000), presumably because animals search for more accessible forage.

(b) *Anthelmintic experiment and parasite abundance*

Two anthelmintic treatments were used across the 6 years. In April 1995 we used only a slow-release abendazole bolus (Proftril, Pfizer) delivered by mouth to the rumen. In April 1996 and 1997, we used only a single-dose injection of moxidectin (Cydectin, Fort George: 0.2 mg kg⁻¹ live weight). In both these years every other animal was treated, with the controls receiving nothing. Since 1998 we have treated one-third of animals with both an ivermectin bolus (Ivomec Maximizer, MSD Agvet) and the injectable moxidectin, one-third with moxidectin only, with the remaining one-third being controls. As described in Irvine (2000) and Irvine *et al.* (2000) moxidectin was efficient at removing worm burdens and keeping egg counts low over the 24 weeks post-treatment.

We counted the abundance of the trichostrongyle nematode species in the abomasa of the reindeer shot in October (see Irvine *et al.* 2000). However, since only *O. gruehneri* appeared to

be pathogenic (Stien *et al.* 2002), and only the abundance of *O. gruehneri* varies between years (Irvine *et al.* 2000), we did not include *M. marshalli* in this analysis.

(c) *Analysis of fecundity*

Pregnancy status was investigated in April–May in live caught animals each year using the progesterone (P_4) concentration in blood samples and ultrasound diagnosis (Ropstad *et al.* 1999). The calf production was recorded by the presence of a calf between 25 June and 25 August. The latest we observed a newborn calf was 18 June; thus by starting the census period at 25 June most cases of neonatal mortality would have been recorded as unsuccessful calving. Subsequent calf mortality over the calves' first summer is invariably very low (less than 1%; Reimers 1983; Tyler 1987, personal observation) so the timing of the summer observation of the presence of a calf is irrelevant. Information on both pregnancy and calf production was obtained on 35% of the individuals in a given year, while only one of these variables was observed for the rest of the females. The data were analysed using a multinomial model with a logit link (McCullagh & Nelder 1989) to estimate the two parameters p_1 , the probability of a female reindeer being pregnant, and p_2 , the probability of a reindeer having a calf given that it was pregnant. Likelihood ratio tests and profile likelihood confidence limits were used to identify significant effects of explanatory variables (treatment, year and winter precipitation) on p_1 and p_2 (McCullagh & Nelder 1989). The variance and confidence limits for the estimated probability of having a calf, $p(\text{calf}) = p_1 p_2$ (called calf production), and the difference in $p(\text{calf})$ between treated and controls was estimated using a simulation approach. Five thousand random samples were drawn from the probability distribution of each parameter (p_1 and p_2) using a simple rejection/acceptance algorithm (Tanner 1993), with the probability distribution of p_1 and p_2 estimated from their likelihood profiles. Pairs of the independent random samples of p_1 and p_2 were then multiplied to generate the probability distribution of $p(\text{calf})$. Estimates of $p(\text{calf})$ from the multinomial model were related to the previous October abundance of *O. gruehneri* using a generalized linear model, with a constant variance structure and logit link function, but with observations weighted by the inverse of the variance of the estimates of $p(\text{calf})$.

(d) *Analyses of survival*

Analyses of survival were carried out using sightings of individually marked animals during yearly summer censuses of the study area, including the captures in the summer of 1994, and analysed using the standard Cormack–Jolly–Seber survival model (Lebreton *et al.* 1992) with a logit link function in program MARK (White & Burnham 1999). During initial data exploration using U-CARE (Choquet *et al.* 2001), it became clear that adult reindeer had a lower probability of being seen again after the first sighting than after subsequent resightings. This suggests the occurrence of transient animals in the population (Pradel *et al.* 1997). To remove this effect, we based our estimates on animals that were seen at least twice, by removing all first sightings from the dataset. In this reduced dataset, there was no evidence for violations of the model assumption. Our main objective in the analysis was to investigate whether the experimental anthelmintic treatment had an effect on apparent survival over the subsequent winter. In any year, reindeer could belong to one of three groups with respect to experimental treatment: (i) treated; (ii) control; or (iii) not part of the experiment that year. We also distinguished between years and the group of

known-age animals, which were caught as yearlings or calves and therefore all of prime age during the study period (two to seven years), and unknown age animals that were caught as adults (two years or older). The resighting parameter was also allowed to vary between years. Model selection was based on AIC and likelihood ratio tests, and confidence limits for the parameters were estimated using the delta method (White & Burnham 1999).

Previous analyses of the age structure of dead animals have found that survival is high for one- to seven-year-old animals and lower in animals of higher age, with no reindeer older than 17 years being found (Reimers 1983; Tyler & Øritsland 1999; Solberg *et al.* 2001). In our analysis we found evidence for lower survival in unknown age animals than prime age animals that is presumably due to the lower survival of the older animals in the unknown-age group. Information from carcasses that only two ($n_{17} = 2$) out of 196 animals had reached the age of 17 yr was used, and the assumption that

$$n_{17} \sim \text{binomial}(p, 196), \quad (2.1)$$

with the yearly survival of animals aged eight years and older (s_{old}) constant so that $p = (s_{\text{prime}})^7 (s_{\text{old}})^9$, and with s_{prime} estimated in the mark-recapture analysis.

Calves were captured for the first time late in their first winter. The mark-recapture study was therefore unsuitable for estimating over-winter calf survival. However, a crude estimate of calf survival was obtained as $s_0 = Y_t/C_{t-1}$, where Y_t is the number of yearlings counted in the July census of the study area in year t , and C_{t-1} is the number of calves counted during the same survey in the previous year. A reliable count of yearlings was only available for the last three years of the study, and it has to be acknowledged that this estimator is likely to be biased downwards due to the difficulties inherent in distinguishing yearlings and two-year olds.

(e) Analysis of *Ostertagia gruehneri* burdens

Conditional on their respective means μ_{ghij} we assumed that the intensity of *O. gruehneri* infection n_{ghij} in reindeer g , with reproductive status h , sampled in valley i in year j followed a negative binomial distribution, and that the negative binomial variance parameter k was a linear function of the mean (Irvine *et al.* 2000). Thus,

$$n_{ghij} \propto \text{Negbin}(m_{ghij}, k_{ghij} = \alpha_1 + \alpha_2 \mu_{ghij} 10^{-3}). \quad (2.2)$$

The abundance of infection (μ_{ghij}) was assumed to depend on host age following a simple immigration-death model (Halvorsen *et al.* 1999):

$$\mu_{ghij} = M^* (1 - e^{-\beta_{0,i} a g e_j}). \quad (2.3)$$

Variation in the asymptotic abundance of infection with age (M^*) due to differences between the two valleys, reproductive status, year and the continuous variable host density (H_{j-k}) in year $j-k$ was investigated using linear models. Since linear models may give unreasonable predictions outside the observed host density range, we also fitted a theoretically derived function for the expected relationship between parasite abundance and host density. Arneberg *et al.* (1998) derived an expression for the equilibrium abundance of parasites assuming: (i) density-dependent host population growth in the absence of parasites; (ii) that parasite population growth rate is density dependent in the absence of parasite-induced host deaths; (iii) a negative binomial distribution of parasites in the host population; and (iv) that the

dynamics of free-living transmission stages occur over a much shorter time-scale than changes in host and adult parasite populations. Their model can be simplified to the following function:

$$M_{ij}^* = \frac{\beta_{1,i} H_{i(j-k)}}{\beta_2 + H_{i(j-k)}} - \beta_3. \quad (2.4)$$

The difference in abundance found between the two valleys was modelled as a difference in β_1 . All models for the abundance of infection were fitted using maximum likelihood and confidence limits estimated from the likelihood profile (McCullagh & Nelder 1989; Irvine *et al.* 2000). The effect of host density on between-year variation in M^* was evaluated using analysis of deviance (Skalski *et al.* 1993), while likelihood-ratio tests were used for assessing the significance of other predictor variables (McCullagh & Nelder 1989).

(f) Modelling the effects of parasites on reindeer population dynamics

We used a standard Leslie matrix model with nine age classes to model the dynamics of the reindeer population. The model had separate age classes for zero- to seven-year olds and one age class for older animals. We assumed a birth sex ratio of 1 : 1 and no difference in male and female survival. Very few female reindeer have a calf before the age of three years (Langvatn *et al.* 1999) so the fecundity of younger reindeer was assumed to be zero. Effects of winter precipitation (W_t) and the abundance of parasites (M_t) on reindeer fecundity (f_t) were modelled additively,

$$f_t(W_t, M_t) = \max(0, w(W_t) - g(M_t)), \quad (2.5)$$

where w is the function for the estimated relationship between W_t and the calf production of treated reindeer and g is the function for the relationship between M_t and the effect of treatment on the calf production. The abundance of *O. gruehneri* infection was assumed to be related to the host population density by the function for M^* (equation (2.4)):

$$M_t = M^*(H_{t-k}). \quad (2.6)$$

The stochastic variation in birth rates due to winter precipitation was modelled by randomly drawing one observation from the last 21 years of observations of winter precipitation at each time-step, while demographic stochasticity was included by assuming that the number of calves produced, and the number of animals surviving in any year, followed binomial distributions in the model simulations. Model simulations were run for 500 time-steps. Unbounded population growth was determined by a population growth rate, $r = \ln(n_t/n_{t-1})$, significantly higher than 0 over the last 300 time-steps (n is the total reindeer population size). Average population density was calculated using the last 300 iterations, and patterns across simulations that varied with respect to assumed survival were explored using locally weighted regression (Chambers & Hastie 1991).

3. RESULTS

(a) Parasite-mediated host reproduction but not host survival

After accounting for the annual variation (see below), reindeer with anthelmintic treatment were more likely to be pregnant than untreated controls ($\chi^2_1 = 4.92$, $p = 0.03$; figure 1a) with no additional treatment effect on the pro-

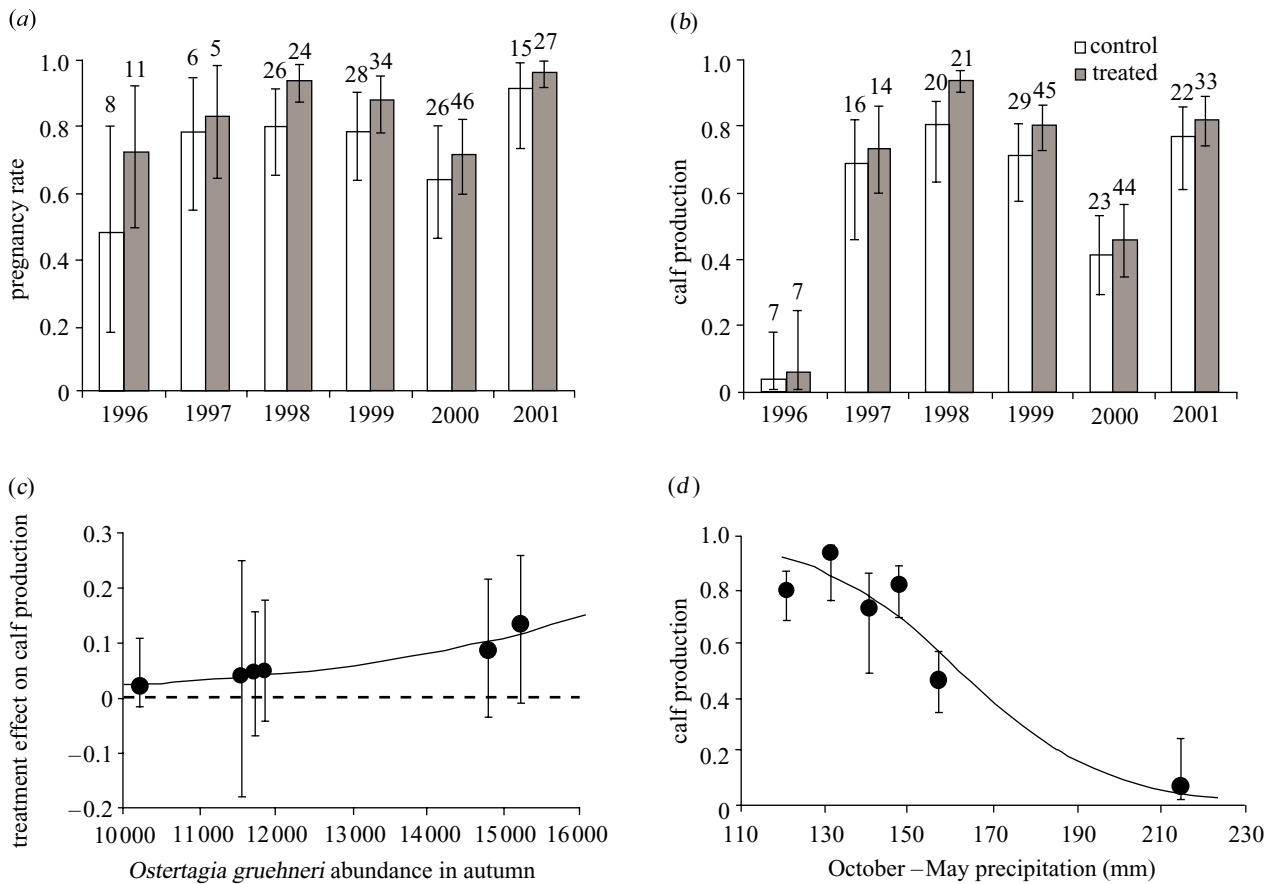


Figure 1. (a) The estimated pregnancy rate in April–May in controls (open bars) and reindeer treated with anthelmintics 12 months earlier (shaded bars). Numbers over the bars give the sample size of animals with pregnancy status determined. (b) The estimated calf production ($p(\text{calf})$) among controls (open bars) and reindeer treated with anthelmintics in April–May the previous year (shaded bars). Numbers over bars give the sample size of animals with the presence or absence of a calf determined. (c) The difference in the calf production of reindeer treated with anthelmintics in the previous April–May and controls, in relation to the estimated *Ostertagia gruehneri* abundance in October (estimated regression line: difference = $1/(1 + \exp(7.025 - 0.000328 \times O. \text{gruehneri abundance}))$). *O. gruehneri* abundances for Colesdalen were estimated as the asymptotic abundance with age (M^* ; equation (2.3)) using the linear model $M^* = \text{valley} + \text{year}$. (d) The calf production among treated reindeer in relation to total winter (October–May) precipitation (estimated regression line: calf production = $1/(1 + \exp(-9.58 + 0.0591 \times \text{winter precipitation}))$). All error bars give 95% confidence limits of the estimates.

portion of pregnant females that had a calf in the summer ($\chi^2_1 = 0.39$, $p = 0.53$; figure 1b). The best estimates of the anthelmintic treatment effect on calf production varied between 0.02, in 1996, and 0.13, in 1998. The magnitude of the treatment effect was significantly positively related to the abundance of adult *O. gruehneri* (M^*) in reindeer sampled in the previous October ($F_{1,4} = 52.91$, $p = 0.002$; figure 1c).

In contrast to reproduction, there was no difference in survival rate between treated individuals and controls ($\chi^2_1 = 0.02$, $p = 0.89$) although there was a weak tendency for treated animals to have higher survival rates than controls (estimated log-odds ratio: 0.09, s.e. = 0.67).

(b) Annual variation in reproduction and survival

There was significant between-year variation in pregnancy rates in April ($\chi^2_5 = 22.72$, $p = 0.001$; figure 1a) and the proportion of pregnant females that were sighted with a calf ($\chi^2_5 = 41.95$, $p = 0.001$; figure 1b). The pronounced between-year variation in calf production was negatively associated with increasing winter precipitation ($F_{1,4} = 28.45$, $p = 0.006$; figure 1d). After correcting for the effect of win-

ter precipitation, there was no evidence of a direct effect of the previous summer's reindeer density on the calf production ($F_{1,3} = 1.60$, $p = 0.30$) and the tendency was towards a positive relationship rather than a negative one (estimated log-odds ratio: 0.75, s.e. = 0.67).

Annual survival differed significantly between prime-age and unknown-age animals ($\chi^2_1 = 8.34$, $p = 0.004$) with prime-age animals having much higher average survival ($s_{\text{prime}} = 0.97$, 95% CI = (0.91, 0.99)) than unknown-age animals ($s_{\text{unknown}} = 0.89$, 95% CI = (0.84, 0.93)). In the prime-age animals there was no evidence for between-year variation in survival ($\chi^2_3 = 3.85$, $p = 0.28$), while the survival of unknown-age animals varied between years ($\chi^2_4 = 9.93$, $p = 0.04$). This between-year variation in the survival of unknown-age animals showed a tendency to be negatively related to winter precipitation (estimated log-odds ratio: -0.014 , s.e. = 0.008), but not to the previous summer's reindeer density (estimated log-odds ratio: -0.12 , s.e. = 0.51). The carcass data gave an estimate of old-age survival (age greater than or equal to eight years) of $s_{\text{old}} = 0.62$ (95% CI = (0.50, 0.69)). Calf survival was estimated to be $s_0 = 0.66$ (s.e. = 0.03).

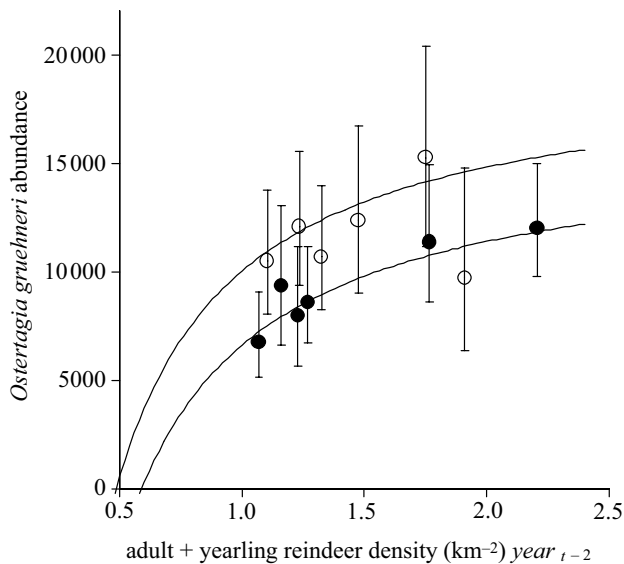


Figure 2. The estimated *Ostertagia gruehneri* abundance in October in relation to adult and yearling reindeer summer density two years earlier in Colesdalen (filled circles) and Sassendalen (open circles). (Estimates for regression lines: $M^* = \beta_{1,i} H_{t-2} / (0.56 + H_{t-2}) - 1\,779\,726$, $\beta_{1, \text{Colesdalen}} = 1\,800\,412$, $\beta_{1, \text{Sassendalen}} = 1\,795\,008$). The valley-specific annual estimates of the abundance of *O. gruehneri* were estimated as the asymptotic abundance with age (M^* , equation (2.3)) using the linear model $M^* = \text{valley} + \text{year} + \text{valley} : \text{year}$. Error bars give 95% confidence limits for the estimates and the sample sizes on which the estimates are based are given above (Colesdalen) or below (Sassendalen) the error bars.

(c) Parasite abundance

The asymptotic abundance of *O. gruehneri* infection (M^*) was significantly higher in Colesdalen than in Sassendalen (estimated difference: 3157 *O. gruehneri*/host, 95% CI = (552, 5918)) and varied between years ($\chi^2_3 = 21.58$, $p = 0.001$), but with no significant valley-year interaction ($\chi^2_4 = 3.26$, $p = 0.51$) and a tendency for a higher abundance of infection in females that were lactating (estimated difference: 1429 *O. gruehneri*/host, 95% CI = (-148, 2923)).

After taking into account the valley differences in the age-intensity relationship, linear models showed that the annual variation in the asymptotic abundance of infection (M^*) was not significantly related to host density in *year_t*, or *year_{t-1}* ($p > 0.70$), but to the host density in *year_{t-2}* (analysis of deviance: $F_{1,9} = 17.98$, $p = 0.002$). There was no evidence of a difference between the valleys in the slope of the M^* -host density relationship (ANODEV test for valley-density interaction: $F_{1,8} = 0.64$, $p = 0.45$). The non-linear model for the M^* -host density relationship (equation (2.4)) gave a slightly better fit to the data than the linear model (difference in 2log-likelihood = 1.0), supporting the use of this biologically more reasonable model (figure 2).

(d) Population consequences of parasites

The model with both density-dependent parasite-mediated effects and stochastic weather effects on the calf production, and a constant prime age survival of $s_{\text{prime}} = 0.97$ (for reindeer of age one to seven years), pre-

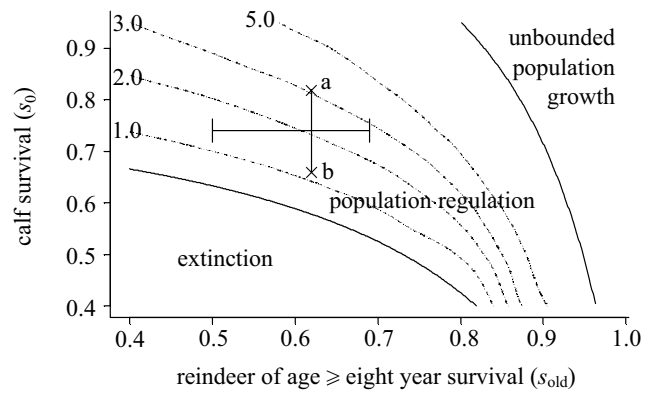


Figure 3. Summary of the output from the matrix model of the Svalbard reindeer population dynamics using the range of possible values of annual calf survival and the annual survival of reindeer more than or equal to eight years old (s_{old}). Prime-age survival (age one to seven years) was assumed constant at the estimated value, $s_{\text{prime}} = 0.97$. Bold lines give boundaries between the parameter space where the host population becomes extinct and where the host population is regulated, and where the host population is regulated and shows unbounded growth. Dotted lines give the combination of parameter values in the regulated zone that give an average adult + yearling population density of 1, 2, 3 and 5 reindeer km^{-2} . The horizontal bar gives the 95% confidence interval for the estimate of s_{old} . The crosses connected with a line give the estimates for annual calf survival (a) in Tyler & Øritsland (1999), (b) in this study, at the estimated $s_{\text{old}} = 0.62$.

dicted that the reindeer population would become extinct if both calf and old-age survival were low (figure 3). At $s_{\text{old}} = 0.62$, calf survival needed to be at least 0.58 to stop the population from becoming extinct. At higher survival rates, the population persists with regulation at increasingly higher mean reindeer densities until it escapes into unbounded growth. Estimates of the annual calf survival vary between 0.66 (this study) and 0.82 (Tyler & Øritsland 1999) and at the estimated $s_{\text{old}} = 0.62$ predicted average host population densities in the range of observed densities (1.1–3.1 reindeer km^{-2}). Without the parasite effect on calf production in the model, there is no population regulation even though a random walk close to the extinction boundary may cause the population to persist at low numbers for extended periods of time. For $s_{\text{old}} = 0.62$, the model predicted a population growth rate in the absence of the parasite of 1.6% yr^{-1} with a calf survival rate of 0.66 and 5.7% yr^{-1} with a calf survival rate of 0.82. With a parasite-mediated reduction in calving rate greater than 0.05, the population growth rate would become negative at a calf survival rate of 0.66 while a parasite-mediated reduction in the calf production of 0.14 was needed for a negative population growth rate at a calf survival rate of 0.82. Simulations with constant winter precipitation also showed that the effect of the parasite in this model is stabilizing with no evidence for cyclic dynamics in the regulated range of parameter space. Also, the model predictions were insensitive to the length, in years, of the time-delay in the response of the parasite abundance to host densities.

4. DISCUSSION

We have found evidence, for the first time in a mammalian herbivore, consistent with the theory that a macroparasite can regulate a host population in the natural environment. The anthelmintic experiment showed that the parasitic nematode *O. gruehneri* decreased fecundity but not the survival of reindeer. This parasite-mediated reduction in calf production was density dependent, increasing with the annual mean estimate of *O. gruehneri* abundance in the host population. In turn, the abundance of *O. gruehneri* was density dependent with a delayed positive response to changes in host densities. Incorporating these host–parasite interactions explicitly into a model demonstrated that parasites were sufficient to regulate the reindeer host population.

(a) *Contrasting effects of parasites on fecundity and survival*

In recent years, several experimental studies have shown that macroparasites can have a negative effect on host fecundity and survival (reviewed in Gulland 1995). However, until our study, only the research on red grouse and *Trichostrongylus tenuis* (Dobson & Hudson 1992; Hudson *et al.* 1992) provided an estimate of the functional relationship between worm burden and parasite pathogenicity in a natural vertebrate population. Our estimates of the costs of parasites are almost certainly conservative because animals treated with moxidectin became re-infected after about six weeks (Irvine 2000), suggesting that the effect of *O. gruehneri* may be higher than observed in the experiment. Nonetheless a parasite-mediated reduction in the calf production in the range 5–14% was sufficient to cause a negative population growth rate in the model. By contrast, the median parasite-mediated reduction in hatching success among red grouse was 19% over a period of eight years, and parasites also affected survival. The regulatory effect of such a small parasite-mediated reduction in fecundity in reindeer is possible because the predicted average host population growth rate is inherently low (1–5%) in an environment where winter precipitation has a strong influence on host calf production. Clearly, recognizing the influence of this density-independent factor is important for the interpretation of the potential dynamical effects of the density-dependent factor.

In this experiment we found no clear evidence for a negative effect of the parasites on host survival. Although population growth rate is sensitive to small effects on adult survival, any effect on host survival is likely to be smaller than the effect on host fecundity and therefore difficult to detect statistically (Gaillard *et al.* 2000).

(b) *Time-lags in the abundance of parasites and hosts*

Our model of the relationship between host and parasite abundance is simple, but explicitly incorporates important characteristics of parasite–host relationships, in particular: (i) a decreasing numerical response in worm burdens with increasing host densities (Dobson 1990; Arneberg *et al.* 1998); (ii) a time-delay in the response of the parasite to changing host densities (May & Anderson 1978; Dobson & Hudson 1992); and (iii) a threshold host density

below which the parasite becomes extinct (May & Anderson 1979). The long time-lag between changes in host and parasite population densities found in our study is likely to be due to the strong seasonality in the Arctic. Due to their temperature-dependent development (Smith *et al.* 1986), the short, cold, Arctic summers retard the development of eggs released on pasture and may delay the appearance of infective larvae until the following summer. Furthermore, after infection most of the larvae may spend another winter arrested in the host before development into reproducing adults (Gibbs 1986). Early theoretical studies show that delayed density-dependent factors tend to cause instability in the population dynamics of the host (May 1981). However, recent studies show that the destabilizing effect of the parasite can be small in systems where the host has a strong seasonality in reproduction (White *et al.* 1996). Analyses of our model suggest that only minor changes are generated in simulated dynamics when the time-lag in the response of the parasite to changes in host population densities is reduced from two to one year. This is due to the inability of the parasite to cause a strong over-compensatory effect on host population growth rate. The main cause of fluctuations in reindeer numbers in the simulation model is stochastic environmental effects on birth rates.

(c) *Stochastic weather effects*

Our finding that calf production was negatively related to total winter precipitation is consistent with the conclusions from the analysis of annual summer population counts over 21 years in the same area (Solberg *et al.* 2001). Also, the effect of winter precipitation on reindeer fecundity may explain why the annual population growth rate of a herd introduced in 1978 to Brøggerhalvøya, ca. 100 km northwest, was low after winters with high precipitation (Aanes *et al.* 2000). High precipitation in winter, and the associated accumulation of snow, potentially increases the costs of locomotion and makes food less accessible (Fancy & White 1985; Adamczewski *et al.* 1988), thereby reducing the nutritional condition of pregnant females and their ability to give birth to a viable calf. In support of this proposal, we have shown that in 1996, the year with highest winter precipitation and lowest calf production in our study, female reindeer were, on average, 25% lighter in April than in either the previous or subsequent winters (Säkkinen *et al.* 2001). The lightest females in April 1996 were also least likely to be pregnant, or if pregnant they were more likely to have a dead foetus (Langvatn *et al.* 1999).

(d) *Combining experimental and observational approaches*

Our success in demonstrating a parasite-mediated density-dependent reduction in the proportion of females with a calf was only possible because we repeated the experiment in each of 6 years, which enabled us to tease out the confounding effects of the stochastic variation in winter precipitation (Jonzén *et al.* 2002). The only other study, to our knowledge, to demonstrate parasite-mediated regulation of a natural population, the *T. tenuis*–red grouse system in northern England, was conducted over eight years (Hudson *et al.* 1992). Thus, the paucity of examples demonstrating the role of parasites in the regulation of host

populations may be largely a function of the short duration of many studies. Furthermore, our demonstration of the potential for parasite-mediated host regulation may be attributable to the relative simplicity of our model system, in which there are few confounding factors. However, our results do not discount the possibility that other density-dependent mechanisms are involved, in particular, through forage limitation. Unfortunately, since food availability is difficult to manipulate in the wild, both at the population and the individual reindeer level, only long-term correlational studies can detect the effects of variation in forage biomass on population performance. Also, the inherent difficulties in measuring food availability, and the fact that primary production varies with the prevailing weather conditions, means that the direct link between population performance and forage biomass has rarely been demonstrated. All too commonly it is assumed as an explanation of why vital rates decline with increasing population sizes (Sæther 1997). It is also likely that the impact of parasites interacts with both winter weather and the productivity of forage species in summer. However, quantifying these interactions is a continuing challenge to ecologists.

The authors are grateful to the Governor of Svalbard for permission to work on Spitsbergen and for the support of his environmental staff, in particular, Jon Ove Scheie. At the outset, essential logistical support and equipment hire was through the Norwegian Polar Institute. More recently Fred Skancke Hansen and Jørn Dybdahl have provided these services at UNIS. Spring catching trips involved additional help from Erling Meisingset, Inge Engeland, Irma Oskam, Jan Licke, Leif Egil Loe, Glenn Roar Berge, Yvonne Halle, Steeve Côté, Chantal Beaudoin, Andrew Read and Elke Lindner, and the subsequent summer follow-up included Steve Wilkinson, Erling Meisingset, Veibjørn Veiberg, Leif Egil Loe, Johan Andersen, Chris McFarlane, Jules Jones and Fanni Aspetsberger. The authors very much appreciate all their contributions. Discussions with Laurent Crespin and David Elston helped improve the statistical analyses, and the comments of Peter Hudson and an anonymous referee helped to refine the arguments. The work was funded both by the Research Council of Norway (TERRØK programme 1994–1996, and Arktik Lys programme 1996–1999) and the Natural Environment Research Council, UK (1997–2000: GR3/10811).

REFERENCES

- Aanes, R., Sæther, B.-E. & Øritsland, N. A. 2000 Fluctuations of an introduced population of Svalbard reindeer: the effects of density-dependence and climatic variation. *Ecography* **23**, 437–443.
- Adamczewski, J. C., Gates, C. C., Soutar, B. M. & Hundson, R. J. 1988 Limiting effects of snow on seasonal habitat use and diets of caribou (*Rangifer tarandus greolandicus*) on Coat Island, North West Territories, Canada. *Can. J. Zool.* **66**, 1986–1996.
- Anderson, R. M. & May, R. M. 1978 Regulation and stability of host–parasite population interactions. I. Regulatory processes. *J. Anim. Ecol.* **47**, 219–247.
- Arneberg, P., Skorping, A., Grenfell, B. & Read, A. F. 1998 Host densities as determinants of abundance in parasite communities. *Proc. R. Soc. Lond. B* **265**, 1283–1289. (DOI 10.1098/rspb.1998.0431.)
- Bye, K. & Halvorsen, O. 1983 Abomasal nematodes of the Svalbard reindeer (*Rangifer tarandus platyrhynchus* Vrolik). *J. Wildl. Dis.* **19**, 101–103.
- Chambers, J. M. & Hastie, T. J. 1991 *Statistical models in S*. New York: Chapman & Hall.
- Choquet, R., Reboulet, A.-M., Pradel, R. & Lebreton, J.-D. 2001 *U-CARE (Utilities—capture—recapture) user's guide*. Montpellier: Typoskript CEFE/CNRS.
- Dallas, J. F., Irvine, R. J., Halvorsen, O. & Albon, S. D. 2000 Identification by polymerase chain reaction (PCR) of *Marshallagia marshalli* and *Ostertagia gruehneri* from Svalbard reindeer. *Int. J. Parasitol.* **30**, 863–866.
- Dobson, A. P. 1990 Models for multi-species parasite–host communities. In *Parasite communities: patterns and processes* (ed. G. Esch, A. O. Bush & J. M. Aho), pp. 261–288. London: Chapman & Hall.
- Dobson, A. P. & Hudson, P. J. 1992 Regulation and stability of a free-living host–parasite system: *Trichostrongylus tenuis* in red grouse. II. Population models. *J. Anim. Ecol.* **61**, 487–498.
- Fancy, S. G. & White, R. G. 1985 Energy expenditure of caribou while cratering in snow. *J. Wildl. Mgmt* **49**, 987–993.
- Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A. & Toïgo, C. 2000 Temporal variation in fitness components and population dynamics of large herbivores. *A. Rev. Ecol. Syst.* **31**, 367–393.
- Gibbs, H. C. 1986 Hypobiosis in parasitic nematodes—an update. *Adv. Parasitol.* **25**, 129–174.
- Gulland, F. M. D. 1995 The impact of infectious diseases on wild animal populations: a review. In *Ecology of infectious diseases in natural populations* (ed. B. T. Grenfell & A. P. Dobson), pp. 20–51. Cambridge University Press.
- Halvorsen, O. & Bye, K. 1986 Parasitter i Svalbardrein 1. Rundmark i løpen (in Norwegian). In *Svalbardreinen og dens livsgrunnlag* (ed. N. A. Øritsland), pp. 120–133. Oslo, Norway: Universitetsforlaget.
- Halvorsen, O. & Bye, K. 1999 Parasites, biodiversity and population dynamics in an ecosystem on the high arctic. *Vet. Parasitol.* **84**, 205–227.
- Halvorsen, O., Stien, A., Irvine, J., Langvatn, R. & Albon, S. 1999 Evidence for continued transmission of parasitic nematodes in reindeer during the Arctic winter. *Int. J. Parasitol.* **29**, 567–579.
- Hudson, P. J. 1986 The effect of a parasitic nematode on the breeding production of red grouse. *J. Anim. Ecol.* **55**, 85–92.
- Hudson, P. J. & Dobson, A. P. 1995 Macroparasites: observed patterns. In *Ecology of infectious diseases in natural populations* (ed. B. T. Grenfell & A. P. Dobson), pp. 144–176. Cambridge University Press.
- Hudson, P. J., Dobson, A. P. & Newborn, D. 1985 Cyclic and non-cyclic populations of red grouse: a role for parasitism? In *Ecology and genetics of host–parasite interactions* (ed. D. Rollinson & R. H. Anderson), pp. 77–89. London: Academic.
- Hudson, P. J., Newborn, D. & Dobson, A. P. 1992 Regulation and stability of a free-living host–parasite system: *Trichostrongylus tenuis* in red grouse. I. Monitoring and parasite reduction experiments. *J. Anim. Ecol.* **61**, 477–486.
- Hudson, P. J., Dobson, A. P. & Newborn, D. 1998 Prevention of population cycles by parasite removal. *Science* **282**, 2256–2258.
- Irvine, R. J. 2000 Use of moxidectin treatment in the investigation of abomasal nematodiasis in wild reindeer (*Rangifer tarandus platyrhynchus*). *Vet. Rec.* **147**, 570–573.
- Irvine, R. J., Stien, A., Halvorsen, O., Langvatn, R. & Albon, S. D. 2000 Life-history strategies and population dynamics of abomasal nematodes in Svalbard reindeer (*Rangifer tarandus platyrhynchus*). *Parasitology* **120**, 297–311.
- Jonzén, N., Lundberg, P., Ranta, E. & Kaitala, V. 2002 The irreducible uncertainty of the demography–environment interaction in ecology. *Proc. R. Soc. Lond. B* **269**, 221–225. (DOI 10.1098/rspb.2001.1888.)
- Langvatn, R., Albon, S. D., Irvine, R. J., Halvorsen, O. & Rop-

- stad, E. 1999 Parasitter, kondisjon og reproduksjon hos Svalbardrein (in Norwegian). In *Svalbardtundraens økologi* (ed. S. Parasitter, F. Mehlum & T. Severinsen), pp. 139–147. Tromsø: Norsk Polarinstitutt mdelelser nr. 150.
- Lebreton, J.-D., Burnham, K. P., Clobert, J. & Anderson, D. R. 1992 Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* **62**, 67–118.
- McCullagh, P. & Nelder, J. A. 1989 *Generalized linear models*. London: Chapman & Hall.
- May, R. M. 1981 Models for single populations. In *Theoretical ecology: principles and applications*, 2nd edn (ed. R. M. May), pp. 5–29. Oxford: Blackwell Scientific.
- May, R. M. & Anderson, R. M. 1978 Regulation and stability of host–parasite population interactions. II. Destabilising processes. *J. Anim. Ecol.* **47**, 249–267.
- May, R. M. & Anderson, R. M. 1979 Population biology of infectious diseases: Part II. *Nature* **280**, 455–461.
- Pradel, R., Hines, J. E., Lebreton, J.-D. & Nichols, J. D. 1997 Capture–recapture models taking account of transients. *Biometrics* **53**, 60–72.
- Reimers, E. 1982 Winter mortality and population trends of reindeer on Svalbard. *Arctic Alpine Res.* **14**, 295–300.
- Reimers, E. 1983 Mortality in Svalbard reindeer. *Holarctic Ecol.* **6**, 141–149.
- Ropstad, E., Johansen, O., King, C., Dahl, E., Albon, S. D., Langvatn, R. L., Irvine, R. J., Halvorsen, O. & Sasser, G. 1999 Comparison of plasma progesterone, transrectal ultrasound and pregnancy specific proteins (PSPB) used for pregnancy diagnosis in reindeer. *Acta Vet. Scand.* **40**, 151–162.
- Säkkinen, H., Stien, A., Holand, Ø., Hove, K., Eloranta, E., Saarela, S. & Ropstad, E. 2001 Plasma urea, creatinine, and urea:creatinine ratio in reindeer (*Rangifer tarandus tarandus*) and in Svalbard reindeer (*Rangifer tarandus platyrhynchus*) during defined feeding conditions and in the field. *Physiol. Biochem. Zool.* **74**, 907–916.
- Sæther, B.-E. 1997 Environmental stochasticity and population dynamics of large herbivores: a search for the mechanisms. *Trends. Ecol. Evol.* **12**, 143–149.
- Skalski, J. R., Hoffman, A. & Smith, S. G. 1993 Testing the significance of individual- and cohort-level covariates in animal survival studies. In *Marked individuals in the study of bird populations* (ed. J.-D. Lebreton & P. M., North), pp. 9–28. Berlin: Birkhäuser.
- Smith, G., Grenfell, B. T. & Anderson, R. M. 1986 The development and mortality of non-infective free-living stages of *Ostertagia ostertagi* in the field and in laboratory culture. *Parasitology* **92**, 471–482.
- Solberg, E. J., Strand, O., Jordhøy, P., Aanes, R., Loison, A., Sæther, B.-E. & Linnell, J. D. C. 2001 Density dependent and density independent effects on the dynamics of a Svalbard reindeer herd. *Ecography* **24**, 441–451.
- Stien, A., Irvine, R. J., Langvatn, R., Ropstad, E., Halvorsen, O. & Albon, S. D. 2002 The impact of gastrointestinal nematodes on wild reindeer: experimental and cross-sectional studies. *J. Anim. Ecol.* (In the press.)
- Tanner, M. A. 1993 *Tools for statistical inference*. New York: Springer.
- Tyler, N. J. C. 1987 Natural limitation of the abundance of the high Arctic Svalbard reindeer. PhD thesis, University of Cambridge.
- Tyler, N. & Øritsland, N. A. 1989 Why don't Svalbard reindeer migrate? *Holarctic Ecol.* **112**, 369–376.
- Tyler, N. & Øritsland, N. A. 1999 Varig ustabilitet og bestandsregulering hos Svalbardrein (in Norwegian). In *Svalbardtundraens økologi* (ed. S.-A. Bengtson, F. Mehlum & T. Severinsen), pp. 139–147. Tromsø: Norsk Polarinstitutt mdelelser nr. 150.
- White, G. C. & Burnham, K. P. 1999 Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**, S120–S139.
- White, K. A. J., Grenfell, B. T., Hendry, R. J., Lejeune, O. & Murray, J. D. 1996 Effect of seasonal host reproduction on host–macroparasite dynamics. *Math. Biosci.* **137**, 79–99.
- Wegener, C. & Odasz-Albrigtsen, A. M. 1998 Do Svalbard reindeer regulate standing crop in the absence of predators? A test of the 'exploitation ecosystems' model. *Oecologia* **116**, 202–206.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.