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# Seasonal infection patterns in Willow Grouse (*Lagopus lagopus* L.) do not support the presence of parasite-induced winter losses

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We examined the hypothesis that endoparasites of Willow Grouse (*Lagopus lagopus* L.) affect host winter losses, by examining two samples of Willow Grouse collected in early autumn and late winter. Body condition of juvenile birds improved from September to February, but parasite-induced host mortalities among hosts in poor condition were probably not the cause. If heavily infected hosts were removed disproportionately from the host population, the number of parasite species per host together with their prevalence and intensities should be lower in winter than in autumn. While overall parasite burden was lower in winter than in autumn, most parasite species showed no seasonal decrease in prevalence or intensities. Only one species, *Trichostrongylus tenuis*, showed a seasonal decrease in both prevalence and intensity. Mean intensities of *Eimeria* spp. decreased significantly between seasons, while prevalence did not. If mortality rates were higher among heavily infected hosts, parasite aggregation should be lower in winter than in autumn, but no such pattern was found, except for *Eimeria* spp. Thus, the results presented in this study yield no clear evidence for parasite-induced mortality in Willow Grouse between autumn and late winter.

## 1. Introduction

Density fluctuations are a typical feature of many tetraonid populations, where several species exhibit cyclic population dynamics in at least some parts of their ranges (Lindström 1994, Moss & Watson 2001). Among the demographic factors driving these fluctuations, breeding production and over-winter survival stand out as the more important (Steen & Erikstad 1996, Moss & Watson 2001). Winter losses may be large in Willow Grouse; average estimates of winter loss (i.e. August to April) were 46% in adult and 68% in juvenile Willow Grouse in northern Norway (Myrberget 1988). Winter mortality did not correlate with the microtine population density (used as a proxy for predation pressure), nor did the results agree with the hypothesis that depleted or inaccessible food resources inflict a varying but density-dependent mortality rate (Lack 1966). Winter losses were probably not associated with dispersal, as Willow Grouse is rather sedentary (Myrberget 1976, Pedersen *et al.* 1983, Holmstad *et al.* 2004).

In a reanalysis of Myrbergets (1988) data set, Steen and Erikstad (1996) found that winter survival of juveniles had the largest impact on the population growth rate. Thus, winter losses are a crucial factor in Willow Grouse population dynamics, but the causes of variable winter loss are not explicitly identified.

Specialist natural enemies like parasites could act to generate fluctuations, and even regulate populations, through effects on host breeding and survival (Tompkins & Begon 1999). In a 10 years study of British Red Grouse (*Lagopus lagopus scoticus*), winter loss was the key factor determining changes in grouse numbers, and the relative survival of red grouse was significantly increased among birds treated with anthelmintics that reduced the population size of the caecal nematode *Trichostrongylus tenuis* (Hudson 1992). More recently a large scale and replicated field experiment was conducted by Hudson *et al.* (1998), showing that application of anthelmintics that aimed at reducing burdens of *T. tenuis* dramatically altered host dynamics and reduced red grouse population declines.

It has been suggested that microparasites of the genus *Eimeria* may have caused extensive host mortality and grouse population declines in Norway (Brinkmann 1926). However, macroparasites usually cause morbidity rather than mortality in their hosts (Tompkins *et al.* 2002). Sub-lethal effects of parasitism may include reductions in body mass or condition due to the resource drainage imposed by parasites, and this might affect over-winter survival or future possibilities for reproduction, as has been shown in other bird populations (e.g. Both *et al.* 1999, Dawson & Bortolotti 2000, Perrins & McCleery 2001, Monrós *et al.* 2002). The effect of parasites on rates of winter loss may be mediated through other natural enemies, because predators may preferentially select infected prey (e.g. Temple 1987, Moore 2002). The interaction between predation and parasite abundance may therefore magnify even small effects on host morbidity induced by parasites, leaving infected hosts more vulnerable to predation (Hudson *et al.* 1992, Packer *et al.* 2003).

In an ongoing long-term study of two Willow Grouse populations in northern Norway, we found that increasing burdens of particular parasite species, as well as the residual parasite community, were associated with reductions in breeding production, host population growth rates, body mass and body condition (Holmstad *et al.* 2005). However, in that study winter samples were not included, but in another study of Willow Grouse both prevalence and intensity of different, intestinal helminth species declined from late summer to autumn, and were practically absent in winter samples (Wissler & Halvorsen 1977). Such a dramatic reduction in parasite burden between late summer and mid-winter may indicate that the more infected hosts died before mid-winter, although it is difficult to disentangle the cause of the decrease in parasite burdens as long as the extent of parasite mortality remains unknown.

A common feature of most metazoan parasites is their tendency to be aggregated within the host population (Crofton 1971, Anderson & Gordon 1982, Shaw & Dobson 1995). Parasite induced host mortality may therefore act to reduce the level of aggregation, if the probability of dying is positively correlated with the intensity of infection. As a consequence, the distribution of parasites should become less aggregated in winter than in autumn. If reduced parasite aggregation is to be taken as an indication of parasite induced winter losses, this relies on the assumption that parasites are present during winter and that parasite mortality and levels of re-infection are low in the host species. The latter should be a reasonable assumption since transmission of parasites in late autumn and winter is likely to be very low, because of snow cover and prevailing temperatures below zero that will halt or delay transmission stage development (e.g. Soulsby 1982).

In this study we used two samples of Willow Grouse, collected in September and February, to investigate whether parasites were associated with winter losses. This hypothesis was examined by exploring the following predictions:

- If parasite burdens are associated with winter losses, parasites assumed to affect grouse fitness should be present not only in autumn, but also in winter.
- If winter losses predominantly occur among

birds in poor body condition, we should observe an improved mean body condition among the birds in the winter sample compared to those sampled in autumn.

- If the most heavily infected hosts are among the ones that contribute to winter losses, the recorded number of parasite species per host together with their prevalence and mean intensities should be lower in late winter than in autumn.
- If parasite-induced winter losses occur, then parasite aggregation should be lower in winter than in autumn.

## 2. Material and methods

### 2.1. Study area

The study area, Nordre Kattfjord (69°40’ N, 18°15’ E), is situated on the island Kvaløya off the north Norwegian coast in Troms County, northern Norway. The Willow Grouse and Rock Ptarmigan (*Lagopus mutus*) populations inhabiting these areas are exposed to hunting both in autumn and winter. Apart from hunters, grouse are preyed upon by generalist predators like Red Foxes (*Vulpes vulpes*), Stoats (*Mustela erminea*), Rough-legged Buzzards (*Buteo lagopus*) and eagles (mainly *Haliaetus albicilla* but occasionally *Aquila chrysaetos*). Birds of prey like Northern Goshawks (*Accipiter gentilis*) and Gyrfalcons (*Falco rusticolus*) are regularly seen preying on grouse in the study area.

### 2.2. Collection of birds and lab procedures

A total of 131 Willow Grouse were collected by hunters in September 1999 and February 2000 in Kattfjord. Birds were shot during walk-up shooting, i.e. unaided by pointing dogs, to avoid sampling bias induced by parasite infections that may alter scent emission of hosts (Hudson *et al.* 1992). The samples consisted of 72 Willow Grouse collected in autumn and 59 collected in winter. Birds were classified as juveniles (2–3 months old in September) or adults (older than 14 months in September) from moulting sequence and pigmentation of the primaries (Steen 1989). There was no difference in the sex or age distribution between the samples ($\chi^2 = 1.59$, d.f. = 3, P = 0.66). Body mass was estimated as total weight minus weight of the crop contents (± 0.1 g.). All birds were examined for parasites according to procedures given in Holmstad and Skorping (1998). All terms describing the parasite populations follow the definitions of Margolis *et al.* (1982).

### 2.3. Data analysis

We used the residuals from a regression of body mass on skull length (as the best measure of structural size) as an index of body condition. This approach has been criticized (Green 2001), but the sample sizes obtained during this study prevented a more detailed analysis of body condition. In addition, the variation in body mass was too small to invoke significant assumptions about the allometric relationship. We used generalized linear models with negative binomial errors to account for the aggregated distribution of parasites within the host population (Wilson and Grenfell 1997), to examine the relationship between the intensity of each parasite species and the index of body condition.

As several parasite species infected the hosts, we wanted to examine the effects of the total parasite load on host fitness by describing the community with a single, relative measure that weighted each parasite equally. We did this by ranking every positive finding separately within each parasite species in groups defined by host age, by assigning a score to the intensity of each parasite count found in individual hosts, where 1 was allotted to the lowest count and then increasing ranks for greater intensities of the parasite species in question. Midranks were used for ties. All zero values were excluded before ranking.

This procedure would thus assign the score zero to a host with no record of parasites. Ranks of counts for each individual parasite species infecting a particular host were summed to reflect both the number of parasite species that infected each host and the relative intensity of infection in that host. This yielded a normally distributed variable for each age group that incorporated the presence of each species, emphasised the relative intensity of that parasite, and tended to reduce the effect of

Table 1. Mean body mass (g) ± standard deviation ($\bar{x}$ ± SD) of Willow Grouse in groups defined by sex and age in Kattfjord during autumn 1999 and winter 2000. Differences in mean body mass were tested with t-tests.

| | Autumn 1999 | | Winter 2000 | | | |
|---|---|---|---|---|---|---|
| | n | $\bar{x}$ ± SD | N | $\bar{x}$ ± SD | t | P |
| Juvenile hens | 20 | 481.6 ± 46.0 | 12 | 522.2 ± 52.3 | –2.3 | 0.03 |
| Juvenile cocks | 14 | 571.2 ± 56.6 | 16 | 607.2 ± 38.3 | –2.1 | 0.048 |
| Adult hens | 15 | 558.5 ± 55.5 | 12 | 536.5 ± 31.4 | 1.2 | 0.22 |
| Adult cocks | 22 | 618.6 ± 44.0 | 19 | 648.3 ± 30.3 | –2.5 | 0.02 |

outliers in parasite intensities.

To detect trends in parasite aggregation patterns, an index of aggregation developed by Poulin (1993) was used. This index, the Discrepancy index (D), quantifies aggregation as the discrepancy between the observed parasite distribution and the hypothetical distribution in which all hosts are used equally and all parasites are in subpopulations of equal size within each host. Values of D are constrained within the limits of 0 to 1, where zero is interpreted as no aggregation and values approaching unity arises when aggregation is at its theoretical limit and all parasites are found in one host. The advantage of using this method over using the aggregation parameter k of the negative binomial is that, unlike k, D is independent of the mean.

## 3. Results

In all groups defined by age and sex, with the exception of adult females, hosts were significantly heavier in the winter sample than in the autumn sample (Table 1). Juvenile Willow Grouse showed a significant increase in body condition indices between September and February, but this trend was not found in adult birds (Fig. 1). Since fat deposits are insignificant in Fennoscandian grouse, deviations from the predicted bodymass for a given structural size is caused by variation in visceral mass, mainly muscle tissues (Myrberget & Skar 1976, Mortensen *et al.* 1985).

There were fewer parasite species per host in the February sample than in the September sample (t = 2.18, d.f. = 129, P = 0.03). Most parasites did

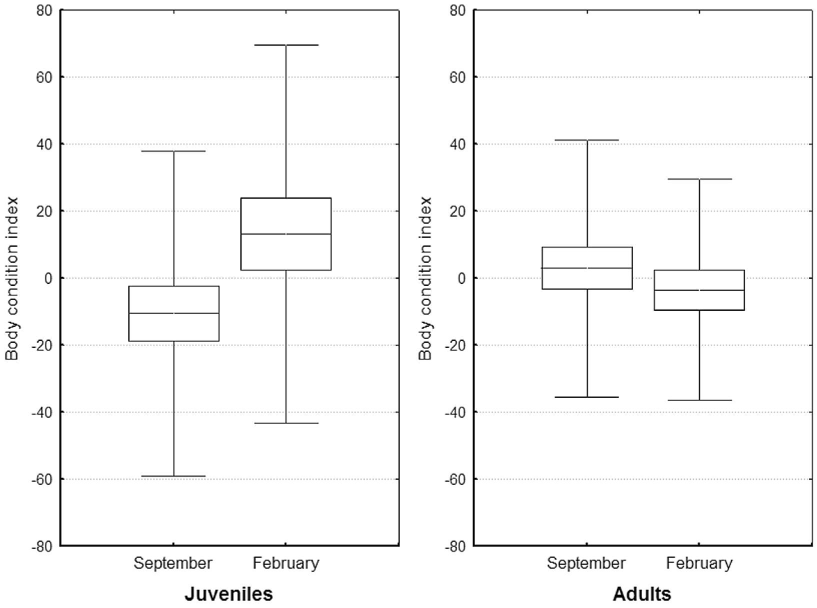


Fig. 1. Differences in Willow Grouse body condition indices between September and February samples (Mean, ☐ denotes Standard Error and whiskers denote ± Standard Deviation). Condition indices were obtained by regressing body mass (dependent variable) against skull length (independent variable). There was a significant difference in condition indices between seasons in juveniles (t = 2.50, d.f. = 61, P = 0.01), but not in adult birds (t = 1.34, d.f. = 66, P = 0.18).

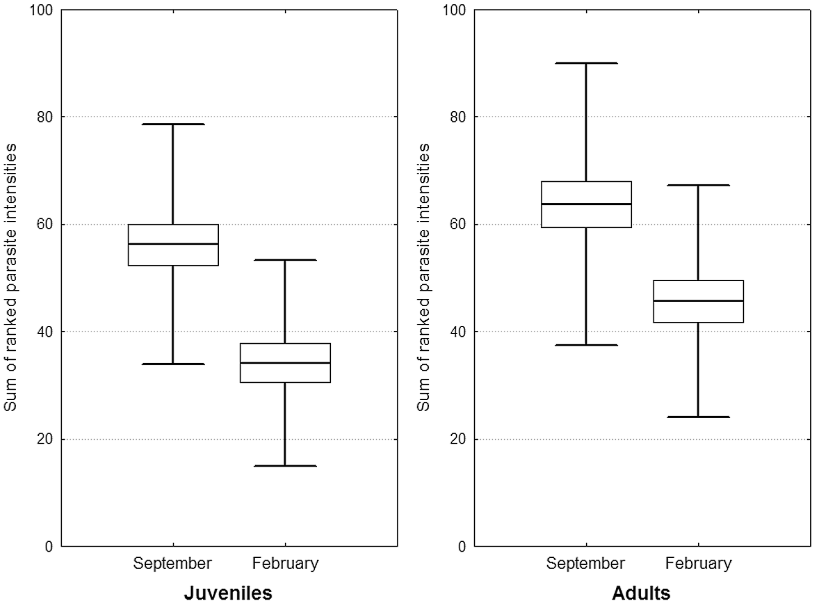
Table 2. Prevalence (Pr) and mean intensities (MI) of all parasite species found in Willow Grouse in Kattfjord during September 1999 and February 2000. Between season differences in prevalence were tested with Yates' corrected $\chi^2$. Between seasons differences in intensities were tested with Mann Whitney U-tests.

| | September 1999<br>(n = 72) | February 2000<br>(n = 59) | Test statistic | P |
|---|---|---|---|---|
| *Eimeria* spp. | Pr 98.6 | Pr 98.3 | 0.00 | 1.00 |
| | MI 11126.8 | MI 1398.8 | 3.51 | 0.0003 |
| *H. microps* | Pr 61.1 | Pr 55.9 | 0.18 | 0.67 |
| | MI 210.2 | MI 187.5 | 0.46 | 0.65 |
| *T. tenuis* | Pr 55.6 | Pr 20.3 | 15.36 | <0.0001 |
| | MI 11.5 | MI 2.3 | 2.62 | 0.009 |
| *P. urogalli* | Pr 12.5 | Pr 22.0 | 1.48 | 0.22 |
| | MI 13.9 | MI 5.1 | –1.38 | 0.17 |
| *S. papillocerca* | Pr 9.7 | Pr 13.6 | 0.17 | 0.68 |
| | MI 2.0 | MI1.3 | –0.75 | 0.45 |
| *C. caudinflata* | Pr 2.8 | Pr 1.7 | 0.00 | 1.00 |
| | MI 2.0 | MI 3.0 | –1.12 | 0.81 |

not show any significant decrease in prevalence or intensities between seasons, except for intensities of *Eimeria* spp. oocysts which were higher in September than in February, and *T. tenuis* which decreased significantly in both prevalence and mean intensity between September and February (Table 2). The sum of ranked parasite intensities was higher in September than in February in both juvenile and adult hosts (Fig. 2). Thus, there were some differences in parasite abundance between seasons, but the abundance of many parasite species remained surprisingly similar between September and February.

Based on earlier findings (Karbøl 1998, Holmstad, Hudson & Skorping 2005), we expected to find a negative correlation between host body condition and parasite burdens. In general no such relationship was found in either season for any of the

Fig. 2. Total parasite burden given as the sum of ranked parasite intensities in individual Willow Grouse hosts (Mean, ☐ denotes Standard Error and whiskers denote ± Standard Deviation). There was a significant difference in ranks between September and February in both juvenile (t = 4.13, d.f. = 61, P = 0.0001) and adult ( t= 3.07, d.f. = 66, P = 0.003) birds.



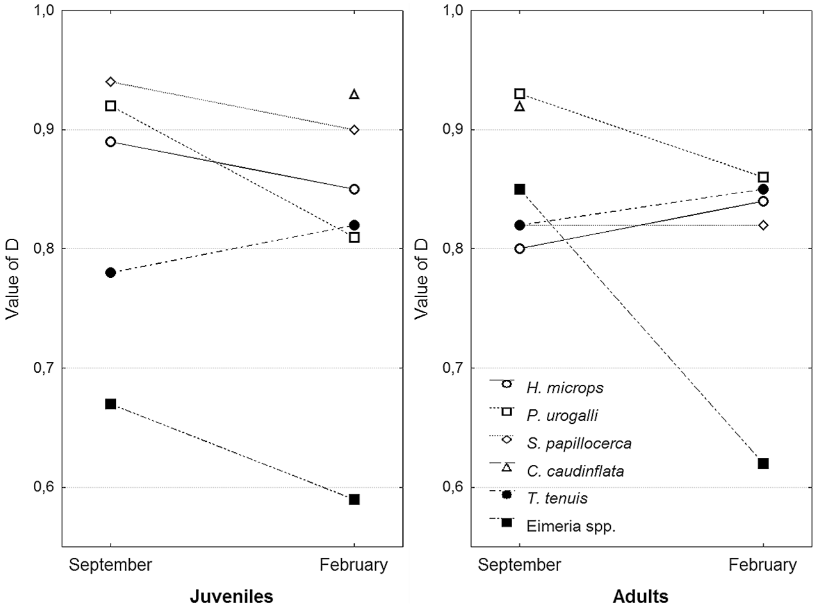


Fig. 3. Changes in the Discrepancy Index "D", a measure of parasite aggregation, between September and February in juvenile and adult Willow Grouse in Kattfjord. Values of D are constrained within the limits 0 and 1. Parasite aggregation increases with increasing values of D.

individual parasite species or total parasite burden expressed as sum of ranked parasite intensities, with the exception of *T. tenuis* in juvenile Willow Grouse ($F_{1,33} = 8.1$, $P = 0.007$). These findings indicate that neither single parasite species nor total parasite burden of hosts was related to host body condition, with the possible exception of *T. tenuis* in juvenile birds, or alternatively; that Willow Grouse were able to compensate for the energy drain imposed by parasite infections.

Patterns of parasite aggregation were not affected by season neither in adult ($t = 0.80$, d.f. = 10, $P = 0.44$) nor juvenile ($t = 0.64$, d.f. = 10, $P = 0.53$) birds. However, oocysts of *Eimeria* spp. showed a lower degree of aggregation in February than in September in both juvenile and adult hosts (Fig. 3).

## 4. Discussion

This study aimed to identify potential parasite-induced winter losses in Willow Grouse. Based on the correlational evidence reported here, we found no indications supporting the hypothesis that parasites had a significant effect on winter mortality. There was a significant improvement of juvenile body condition between September and February, which could have been interpreted as an effect of mortalities among hosts having lower body condition. However, it seems unlikely that parasite induced deaths among heavily infected hosts may have contributed to such seasonal differences in body condition. There was only one significant association between body condition indices and intensities of individual parasite species or total parasite burden; juvenile host condition was negatively related to intensities of *T. tenuis* in September. It is unclear whether this result is biologically sound, because the intensities of *T. tenuis* were very low compared to the English studies on red grouse, where the negative impact of this worm on population dynamics have been demonstrated (e.g. Hudson *et al.* 1998). The lack of relationships between parasite abundance and host body condition was somewhat surprising, since long-term studies from the same area found a clear, negative relationship between these parameters (Karbøl 1998, Holmstad *et al.* 2005).

Hosts were infected by fewer parasite species per host and total parasite burden was lower in winter than in autumn. This is in accordance with the predictions if parasite induced host mortalities removed birds with high parasite burdens disproportionately from the host population. However, among individual parasite species, only *T. tenuis* showed a significant reduction in prevalence and intensities between September and February, and while *Eimeria* spp. had approximately the same prevalence in both seasons, the intensities were significantly lower in winter than in autumn. These findings generally did not support the prediction that parasite-induced host mortalities could have reduced overall parasite burdens at the population level. Moreover, if parasite-induced host mortalities were removing heavily infected hosts selectively, the levels of aggregation in parasite intensities were predicted to be lower in February than in September, but we found no overall reduction in parasite aggregation between seasons. Only *Eimeria* spp. showed a tendency for reduced aggregation in winter.

Earlier studies have indeed suggested that high mortality rates and rapid population declines in Willow Grouse was associated with high burdens of *Eimeria* (Brinkmann 1926). But as microparasite infection parameters may change dramatically over short time intervals, during shifts between chronic and acute phases, the potential effects of microparasites like *Eimeria* may be masked and difficult to detect in field studies like this one (Swinton *et al.* 2002).

Most parasites were present in midwinter, with few detectable differences in infection parameters compared to autumn samples, with the exception of *T. tenuis*. This is in sharp contrast to earlier studies on parasites infecting Willow Grouse, where strong seasonal declines were reported (Huus 1928, Wissler & Halvorsen 1977). In the case of *T. tenuis*, similar seasonal declines in prevalence and intensity have been shown in an earlier study on *Lagopus* spp. (Holmstad *et al.* 2004). Intensities of *Eimeria* spp. oocysts were lower in winter, but prevalence were seemingly unaffected by season, indicating that this microparasitic infection may enter a more chronic stage in winter. This might also apply to the cestode *H. microps*, which showed a marked change in morphology between autumn and winter. This cestode apparently has distinct winter forms generally consisting of a scolex with a few small, non-gravid proglottids attached. These are very different from the long, slender and probably immature forms found in summer and to a lesser extent in autumn, when the mature form of the worm consisting of larger, gravid proglottids predominates (Huus 1928, pers. obs.). This difference in gross morphology might be the reason why Wissler and Halvorsen (1977) failed to identify any *H. microps* in their winter samples of Willow Grouse.

Our findings suggest that parasites like *Eimeria* spp. and *H. microps* over-winter in their host, remaining in a chronic and potentially less pathogenic state. Many other parasite species, e.g. chronic hematozoan infections, also exhibit a phase characterized by exceptionally low intensities of transmission stages in systemic circulation through winter, followed by sudden relapses of infections in spring (Applegate 1991, Atkinson & Van Riper 1991, Valkiûnas *et al.* 2004). This scenario seems likely for blood parasites infecting Willow Grouse (Holmstad *et al.* 2003, Holmstad unpubl.).

In ruminants, nematodes show a general phenomenon called “spring rise”, where intensities rise sharply in spring due to de-arrestment and maturation of the L4 larvae (Wilson *et al.* 2002). In red grouse most of the mortality occurs in spring, as a consequence of mass emergence of arrested *T. tenuis* larvae (Hudson 1992). The mechanisms that governs arrestment and “spring rise” in different parasite species are not adequately understood, but probably include genetic, climatic, and density-dependent processes, as well as effects of reproductive stress and steroid hormones that might compromise host immunocompetence (Schuurs & Verheul 1990, Folstad & Karter 1992, Hillgarth & Wingfield 1997, Wilson *et al.* 2002).

Taken together our study suggests that parasite induced winter losses may be low between fall and midwinter, but potentially increasing in spring because of relapsing infections, indicating that our study did not cover an appropriate time-span for revealing possible parasite induced mortalities. This is in accordance with studies of seasonal mortality patterns of Willow Grouse in Canada, where hens suffered the highest mortality during pre-laying, incubation and pre-fledging brood rearing periods, while peak in male mortality occurred in late winter/early spring during the period of transient territoriality (Hannon *et al.* 2003). Moreover, this particular sampling year (1999) was in many respects unusual, with peaking host densities (Holmstad *et al.* 2005) and findings of several carcasses of grouse chicks during August prior to sampling of the population, with no distinct signs of injury from encounters with predators (pers. comm. by landowners, pers. obs.). This may indicate that the individuals most prone to die due to parasites were already dead when hunting commenced, suggesting that the sampling period might have started too late to get the more heavily infected host individuals. Thus, our results suggest that the bulk of host deaths that can be ascribed directly or indirectly to parasites may occur in other seasons than autumn to late winter. However, experimental evidence where different parasite species are removed from parts of the host population is needed to verify this conclusion.

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## Kausittaiset infektioiden muutokset eivät tue oletusta, että riekon (*Lagopus lagopus*) talvikuolemat olisivat loisten aiheuttamia.

Tutkimme sisäloisten vaikutusta riekon (*Lagopus lagopus*) talvikuolemiin. Nuorten lintujen kunto koheni syyskuusta helmikuulle. Sisäloiset eivät todennäköisesti aiheuttaneet huonokuntoisten yksilöiden kuolemia. Jos linnut, joilla on paljon loisia syksyllä kuolisivat loisten vaikutuksesta, tulisi talvella otetuissa näytteissä olla laji- ja yksilömääräisesti vähemmän loisia kuin syksyllä otetuissa näytteissä. Useimpien loislajien esiintyminen ei kuitenkaan noudattanut em. oletusta.

*Trichostrongylus tenuis* -laji oli ainoa, jonka aiheuttamien infektioiden määrä väheni syksystä talveen samalla, kun infektioiden keskimääräinen voimakkuus pieneni. *Eimeria*-lajien tartuntojen keskimääräiset voimakkuudet laskivat syksystä talveen, mutta esiintyminen ei pienentynyt. Jos voimakkaasti loisitut yksilöt kuolisivat muita helpommin, tulisi talvinäytteissä olla vähemmän loisittuja lintuja kuin syysnäytteissä. Muilla kuin *Eimeria*-suvun sisäloisilla ei tällaista laskevaa trendiä havaittu. Täten tutkimus ei pysty osoittamaan, että riekkojen kuolemat syyskuulta helmikuulle olisivat sisäloisten aiheuttamia.

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