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ABSTRACT: Little is known about the cestode parasites of red grouse *Lagopus lagopus scoticus.* The carcasses of 71 free-living red grouse collected from northeastern Scotland (UK) between June 1991 and September 1992 were examined for the cestode *Paroniella urogalli.* Over 70% of young and old birds were infected in summer and winter. Cestode abundance ranged from 0 to 29 ($\bar{x} \pm$ SE = 5.54 $\pm$ 0.81) worms per host and did not differ significantly between young and old grouse, or between seasons. Cestode intensities did vary significantly between the sexes, but in opposite directions at two sites. A significantly greater total biomass (dry weight) of cestodes was found in grouse in the summer. Cestode biomass also was greater in young than in old grouse, although there was no significant difference after controlling for the effects of site, year and season. However, in the summer total cestode biomass in young grouse was significantly greater per unit bodyweight than in old grouse. No evidence was found for an effect of cestodiasis on grouse condition but a significant positive correlation existed between grouse comb condition and cestode abundance. Estimates of mean per capita worm mass suggested an intensity dependent reduction in the weight of individual cestodes in birds in their first summer. Per capita cestode mass was significantly lower in winter than summer, which may suggest that the production of mature proglottids varies with season. There was also a significant negative correlation between numbers of the nematode *Trichostrongylus tenuis* and the total biomass of *P. urogalli* in grouse.

Key words: Biomass variation, cestodiasis, distribution, helminth ecology, *Lagopus lagopus, Paroniella urogalli,* red grouse.

INTRODUCTION

Despite a growing interest in the epidemiology and ecological consequences of helminth infections in wild vertebrate hosts (reviewed by Grenfell and Gulland, 1995), there have been few field studies on the population biology of cestode infections in birds (Avery, 1969; Dick and Burt, 1971; Goater et al., 1995). In this paper, field data are presented on cestode infections in wild red grouse *Lagopus lagopus scoticus* from Scotland.

The management of red grouse populations for shooting is an important form of land use in the British uplands. Consequently, a broad literature has developed on the biology and management of this gamebird, including its parasites and diseases. The parasitic nematode *Trichostrongylus tenuis* is implicated in outbreaks of 'grouse disease' (Committee of Inquiry, 1911), and, it has been argued, causes cyclic fluctuations in red grouse numbers (e.g., Potts et al., 1984; Hudson et al.,

1992). However, the population biology and potential effects of cestode infections on wild red grouse populations have been largely ignored.

Shipley (1909) examined red grouse from Scotland for cestodes and found that birds were commonly infected with two species. The diminutive *Hymenolepis microps* inhabits the duodenum while the much larger *Davainea urogalli* (synonym of *Paroniella urogalli*) is found in the small intestine, and is described by Shipley (1909) as 'the tapeworm that is familiar' to gamekeepers and sportsmen. Apart from brief descriptions of the prevalence and intensity of infection with this cestode (Shipley, 1909; Committee of Inquiry, 1911; Jenkins et al., 1963; Shaw, 1988), little else is known of it's epidemiology and pathology in red grouse. High intensity infections of *P. urogalli* have been particularly associated with young grouse (Shaw, 1988). Infection is most noticeable in the summer when cestodes can often be seen

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dangling from the anus of birds as they are flushed from cover (Shipley, 1909; R. J. Delahay, pers. obs.).

Little is known of the life cycle of *P. urogalli*, although ingestion of infected arthropod intermediate hosts is the likely route of infection for grouse. Red grouse feed largely on ling heather (*Calluna vulgaris*) but adult grouse, and chicks in particular, supplement this diet with a variety of invertebrates (Committee of Inquiry, 1911; Butterfield and Coulson, 1975; Savory, 1977). However, despite an exhaustive survey of moorland invertebrates (Committee of Inquiry, 1911), *P. urogalli* cysticercoids have only been reported from two species of ant (Formicidae) (Muir, 1954), which paradoxically do not feature strongly in the diet of red grouse (Committee of Inquiry, 1911; Butterfield and Coulson, 1975; Savory, 1977).

The pathological consequences of *P. urogalli* infection in red grouse are unknown. Although several studies have shown little effect of *Davainea* spp. on the growth of galliformes (Taylor, 1933; Dick and Burt, 1971), other workers have described a detrimental effect on weight gain (Harwood and Luttermoser, 1938; Levine, 1938). Shaw (1988) found no relationship between an index of *P. urogalli* abundance and host condition, in a sample of red grouse from several Scottish moorlands. However, as individual cestodes may vary widely in size, total cestode biomass may be a better measure of the parasitic burden imposed on the host than the number of cestodes present.

The objectives of the present study are to describe the prevalence, abundance and biomass of *P. urogalli* in a wild population of red grouse from northeastern Scotland. Variations in the intensity and biomass of cestode infections were related to temporal change and host characteristics.

MATERIALS AND METHODS

Red grouse carcasses were obtained during the summers of 1991 and 1992, and in the intervening winter, from Glen Callater ($n = 39$),

Micras Moor ($n = 25$) and adjacent areas ($n = 7$) on Invercauld Estate, Aberdeenshire, Scotland (UK; approximately 57°6′N, 3°15′W and 56°42′N, 3°20′W, respectively). All sites were ling heather dominated moorlands managed for grouse shooting. All the 71 grouse collected had been shot, except for one which had been killed by a raptor. Grouse collected between 12 August and 1 September were classified as the 'summer sample', and those from 1 December to 1 March as the 'winter sample'. Grouse carcasses were frozen within 2 hr of death, prior to examination.

Plumage and morphological characteristics were used to age and sex grouse (Flux, 1958; Watson and Miller, 1976). Birds in their first year are defined as 'young' and all others as 'old'. Grouse were weighed and their body condition assessed by palpating the sternum musculature and assigning a score on the scale 1 to 15 (emaciated to plump condition) according to muscle mass (Moss et al., 1985). For all male birds, the width and height of one of the supraorbital combs were measured and multiplied together to give an index of comb size. A subjective comb brightness score from one (very dull) to five (very bright) also was allocated. The size and brightness of the comb are positive correlates of social status in red grouse cocks (Moss et al., 1979).

The contents of the small intestine were flushed out by inserting a rubber hose attached to a tap at one end, and passing water through the intestine while gently massaging the contents out over a 500 μm sieve. After flushing, the intestine was cut longitudinally and the inner surfaces rinsed over the sieve. The residue was rinsed thoroughly and washed out onto a shallow plastic tray. Cestodes were collected with forceps and the number of scoleces counted. The often tangled mass of cestodes was rinsed free of debris in warm tapwater prior to drying. The total biomass (dry weight) of cestodes per host was determined by oven drying samples at 80 C to constant weight. For each infected host the mean per capita cestode mass was calculated (total cestode biomass/number of cestodes). As part of a separate study (Delahay, 1995) the abundance of the caecal nematode *T. tenuis* was also recorded for each bird.

Representative cestode specimens were deposited with the Parasitic Worms Division of the British Natural History Museum (London, UK; accession number 1998.6.1.1-5). The samples could only be identified as *Paroniella* sp., but the putative label of *P. urogalli* is ascribed in the present study, as this is the only member of the genus reported from red grouse.

Parasitological terminology in the present paper follows the conventions of Bush et al.

TABLE 1.   Prevalence, mean abundance, variance to mean ratios, total biomass and mean per capita mass of *P. urogalli* in red grouse from Scotland. The larger the variance to mean ratio, the greater the degree of parasite aggregation in the host population. (Note: young birds were those that hatched in the summer of that year).

Age	Season	n	Percentage infected	Cestode abundance ($\bar{x} \pm$ SE)	Variance/mean	Total cestode biomass (g dry weight) ($\bar{x} \pm$ SE)	Per capita cestode mass (g dry weight) ($\bar{x} \pm$ SE)
Young	summer	29	79	6.97 ± 1.42	8.4	0.238 ± 0.045	0.045 ± 0.005
	winter	5	80	6.20 ± 3.10	7.8	0.082 ± 0.058	0.011 ± 0.003
Old	summer	27	71	4.30 ± 1.09	7.5	0.116 ± 0.038	0.036 ± 0.008
	winter	8	87	2.13 ± 0.61	1.4	0.017 ± 0.007	0.007 ± 0.002
Combined	summer	57	75	5.68 ± 0.91	8.2	0.178 ± 0.030	0.041 ± 0.005
	winter	13	84	3.69 ± 1.30	6.0	0.042 ± 0.023	0.009 ± 0.002

(1997). Parasite abundance refers to the number of cestodes present in a host, regardless of whether or not it was infected. Parasite intensity, however, refers to the number of cestodes present in infected hosts only.

Cestode abundance, total biomass and mean per capita cestode mass were not normally distributed (SAS, 1989; UNIVARIATE procedure) and were therefore transformed into normal scores (SAS, 1989; RANK procedure) before inclusion in parametric analyses.

General linear modelling (SAS 1989; GLM procedure) was used to relate variations in normalised cestode abundance, total cestode biomass and mean per capita cestode mass to the explanatory class variables grouse age, sex, season, location (moor), year and all relevant interactions. Cestode abundance was included as a covariate in models investigating total biomass and mean per capita cestode mass. Nonsignificant interactions were removed sequentially from the null model until a final model

comprising the main terms and only those interactions approaching significance ($P < 0.10$) remained. Consequently, the final model controlled for the effects of all the main terms and retained only those interactions of interest, while maximizing the goodness of fit of the model. This approach also avoided the pitfalls of automated stepwise regression procedures which have been criticised for being biologically inappropriate (James and McCulloch, 1990). The residuals for each of the final models were examined and showed no signs of non-normality (see Draper and Smith, 1981).

Relationships between grouse condition score, comb characteristics and cestode abundance were investigated using Pearson's or Spearman's Rank Correlations (SAS, 1989; CORR procedure) and analyses of variance (SAS, 1989; ANOVA procedure) on rank-transformed variables.

RESULTS

Variance to mean ratios indicated that *P. urogalli* was aggregated in the grouse population (Table 1, Fig. 1). Prevalence of infection was high; 79% and 76% in young and old birds respectively. Intensity ranged from 1 to 29 cestodes per infected host, but 48% of infected grouse contained <5 cestodes (Fig. 1). There was no significant difference in the prevalence of infection between grouse collected in winter and summer, between young and old birds or between the sexes (Chi square and Fisher's exact test, $P > 0.05$).

Cestode abundance was greater in young than old grouse, and higher in summer than in winter for both age groups
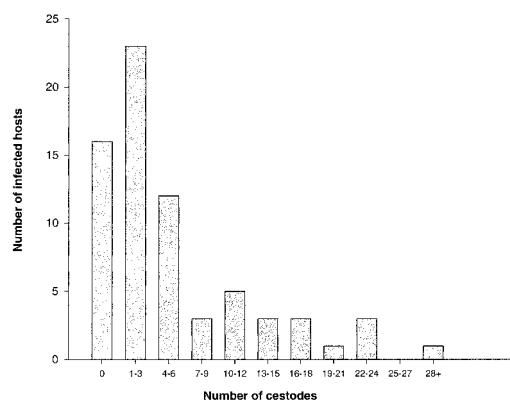

FIGURE 1.   The frequency distribution of *P. urogalli* infections in a wild red grouse population from Scotland.

TABLE 2. Results of general linear models (GLM's) to partition the variation associated with abundance, total biomass and per capita mass (transformed to normal scores) of *P. urogalli* in red grouse.

Dependent variable	P values for independent variables								error d.f.	R^2
	Host age	Host sex	Season	Moor	Year	Age × moor	Sex × moor	Cestode count		
Cestode abundance/host	0.29	0.37	0.33	0.11	0.85		<0.001		50	0.29
Total biomass of cestodes/host	0.08	0.35	0.05	0.57	0.09	0.07		<0.001	49	0.81
Mean per capita cestode mass/host	0.09	0.86	<0.001	0.38	0.01			<0.01	35	0.55
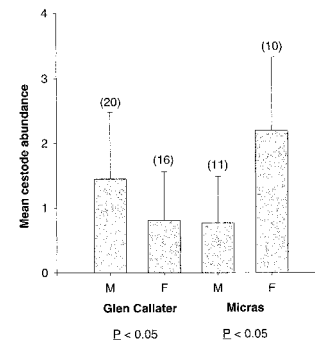
FIGURE 2. Mean abundance of *P. urogalli* in cock and hen red grouse at two moorland sites in north-eastern Scotland (sample sizes are in parentheses).

(Table 1), although these differences were not statistically significant (Table 2). When the GLM analysis was repeated using summer data only, the age related difference in cestode abundance remained nonsignificant ($F_{1,51} = 1.91$, $P > 0.1$). There was, however, a significant association between cestode abundance and the sex × moor interaction (Table 2). Univariate tests showed that at Glen Callater cestode abundance was significantly higher in cock grouse than in hens, whereas at Micras moor hens had more cestodes than cocks (Fig. 2).

There was a borderline significant effect of season on variations in the total biomass of *P. urogalli* per host, independent of cestode intensity (Table 2). Unfortunately, this model could only include total cestode biomass estimates for five birds in winter. However, a univariate test on the original data provided further evidence that total cestode biomass varied significantly with season ($\bar{x} \pm$ SE for winter = 0.04 ± 0.02 g, $n = 13$; for summer 0.18 ± 0.03 g, $n = 57$; *t*-test, $t_{70} = -3.57$, $P < 0.01$).

Total cestode biomass was significantly greater in young birds (*t*-test, $t_{68} = 2.43$, $P < 0.05$; Table 1) although when other factors were controlled in a GLM the effect of age and the age x moor interaction only approached significance (Table 2).

In the summer, old grouse of both sexes were significantly heavier than young birds (*t*-test, $t_{55} = -5.22$, $P < 0.001$; Table 3).

TABLE 3.   Mean grouse bodyweight and relative total biomass of *P. urogalli* in young and adult red grouse in summer (sample sizes are in parentheses).

Age	Grouse bodyweight (g)[a]	Cestode biomass/ host bodyweight (g × 10⁴)[a]
Young	600 ± 11 (29)	4.0 ± 0.8 (29)
Adult	684 ± 12 (28)	2.0 ± 0.6 (28)

[a] $\bar{x}$ ± SE (*n*).

TABLE 4.   The relationship between mean per capita mass and intensity of *P. urogalli* per host, by age and season.

Age	Season	*n*[a]	*R*[b]	*P*[c]
Young	summer	23	−0.55	0.007
	winter	4	0.47	0.53
Old	summer	19	−0.36	0.13
	winter	7	0.34	0.46

[a] *n* = sample size.
[b] *R* = Pearson's Correlation Coefficient.
[c] *P* = probability.

When host bodyweight was controlled in a comparison of cestode biomass in young and old grouse it was shown that the former carried a significantly greater biomass of cestodes per unit bodyweight (*t*-test, t_{57} = 2.39, $P < 0.05$; Table 3).

The mean per capita cestode mass per host varied significantly between seasons (Table 2), being almost five times greater in summer ($\bar{x}$ ± SE = 0.041 ± 0.002 g, *n* = 42) than in winter ($\bar{x}$ ± SE = 0.009 ± 0.005 g, *n* = 11). Per capita cestode mass also showed significant annual variation (Table 2) independently of seasonal differences in sampling over the 2 yr (for summer 1991 $\bar{x}$ ± SE = 0.037 ± 0.005 g, *n* = 45; for summer 1992 $\bar{x}$ ± SE = 0.056 ± 0.013 g, *n* = 12).

Overall, per capita cestode mass was significantly related to cestode intensity (Table 2). However, this relationship was not consistent across seasons and ageclasses (Table 4). There was a strongly significant negative correlation between per capita cestode mass and intensity in young grouse during the summer (Fig. 3) but not for old birds, or in winter (Table 4). However, as a result of the aggregated distribution of *P. urogalli*, heavily infected hosts are under-represented, which may lead to the illusion of density dependence (Keymer and Slater, 1987). In the present study interpretation was aided by comparing the data points with estimated upper and lower 95% confidence limits for mean per capita cestode mass under conditions of no intensity dependent growth. The hypothetical confidence intervals were calculated from a subsample of hosts with infections

of only 1 to 3 cestodes (see Shostak and Scott, 1993). Plotting the data for young grouse in summer over these confidence limits showed that for all hosts with over 10 cestodes, per capita cestode mass fell below the lower 95% confidence limit (Fig. 3).

There was no correlation between grouse condition score and either the abundance or total biomass of cestodes in young or old grouse (Spearman's rank correlations, $P > 0.05$). Total cestode biomass was also unrelated to the size or brightness of the supra-orbital combs of cock grouse (Spearman's rank correlations, $P > 0.05$). However, there was a significant positive relationship between cestode abundance and comb brightness score in cock grouse (Spearman's rank correlation, $R = 0.39$, n
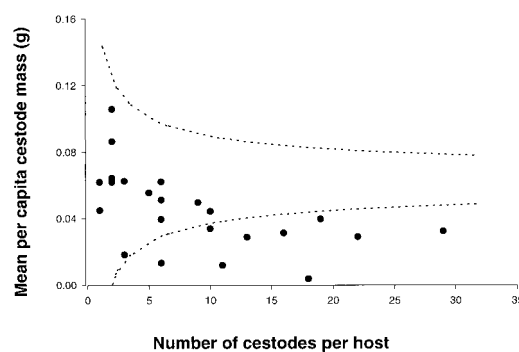

FIGURE 3.   The relationship between the mean per capita mass of *P. urogalli* per host and the intensity of infection, in red grouse in their first summer. Broken lines indicate the extrapolated upper and lower 95% confidence limits for mean per capita cestode mass in grouse infected with only one to three cestodes ($\bar{x}$ ± SE = 0.064 ± 0.009 g).
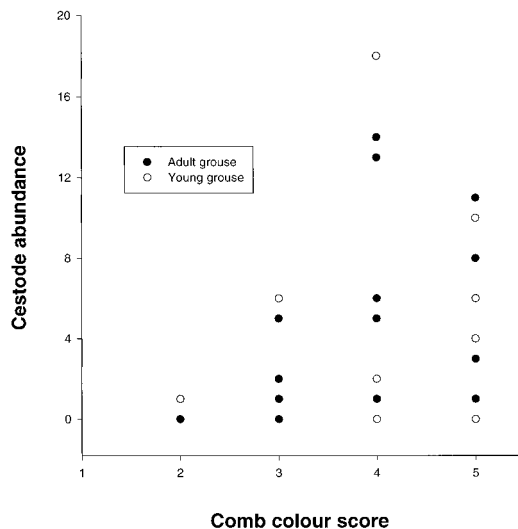
FIGURE 4.   The relationship between red grouse comb brightness score and the abundance of *P. urogalli.*
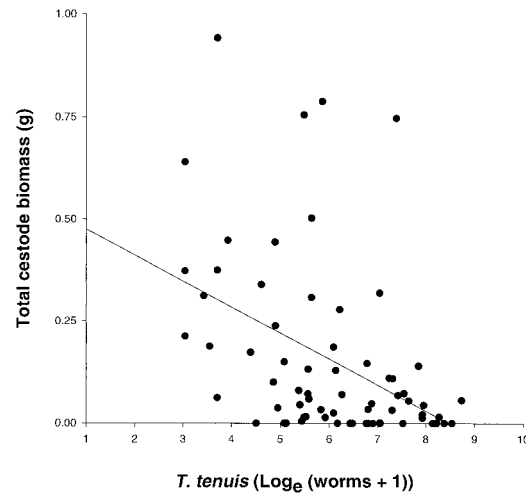

FIGURE 5.   The relationship between the total biomass of *P. urogalli* and abundance of the nematode *Trichostrongylus tenuis* per host (Linear regression, $y = -0.06x + 0.54$, $r^2 = 0.19$, $n = 69$, $P < 0.001$).

$= 35$, $P < 0.05$; Fig. 4). This correlation remained significant after controlling for grouse age and season (ANOVA on ranked scores, $F_{1,31} = 5.8$, $P < 0.05$).

The number of *T. tenuis* nematodes ($\log_e$ (worms + 1)) present in grouse was significantly negatively correlated with the abundance and total biomass of *P. urogalli* (Pearson's correlations, $R = -0.30$, $n = 68$, $P = 0.01$ and $R = -0.43$, $n = 69$, $P < 0.001$ respectively). However, as the acquisition of *T. tenuis* by grouse is cumulative, abundance is higher in adult birds (Wilson, 1979). After controlling for host age there was no significant correlation between the abundance of *T. tenuis* and *P. urogalli* per host (ANOVA, $F_{1,65} = 3.7$, $P > 0.05$) although total cestode biomass remained significantly negatively correlated (ANOVA, $F_{1,66} = 9.0$, $P < 0.01$; Fig. 5).

DISCUSSION

Jenkins et al. (1963) and Shaw (1988) recorded *P. urogalli* in red grouse from Scotland, but unlike the present study made no attempt to determine the factors associated with variations in cestode abundance and biomass. As is characteristic of many helminth infections, the distribution

of *P. urogalli* in the grouse population in the present study was aggregated, with most hosts infected with relatively few cestodes. Prevalence of infection was high (over 70% in young and old birds for both seasons), being at the upper limit of that recorded by Jenkins et al. (1963) (31% to 76% of adult grouse), and did not differ between seasons.

Using an index of cestode abundance, Shaw (1988) found that *P. urogalli* were more numerous in young birds. However, in the present study, although the abundance of *P. urogalli* was indeed greater in young grouse than in old, this difference did not reach statistical significance. This was surprising given the typically insectivorous diet of young grouse in the summer (Committee of Inquiry, 1911; Butterfield and Coulson, 1975; Savory, 1977).

In Norway, willow grouse (*Lagopus lagopus*) are host to *Raillietina urogalli* (=*P. urogalli*) during the summer, but according to Wissler and Halvorsen (1977) are not infected with these cestodes over the winter. This suggests that infected grouse either rapidly lost infections in the absence of reinfection during the colder winter

months, or that the hosts died off as winter approached. In the present study, *P. urogalli* was found in grouse in both seasons and although numbers were lower in winter this difference was not significant, and prevalence of infection remained roughly similar.

However, in the present study mean per capita cestode mass did vary significantly between seasons, cestodes being approximately 320 and 400% heavier in summer than in winter, in young and old grouse respectively. This is consistent with the findings of Dick and Burt (1971) who describe seasonal variation in the presence of two morphs of the cestode *Davainea tetraoensis* in ruffed grouse *Bonasa umbellus.* In their study the smaller non-gravid morph dominated in birds during the winter, and gravid forms with mature proglottids were most abundant in the summer. However, the factors responsible for this phenomenon are unclear. In the present study, the lower mean per capita mass of *P. urogalli* in grouse in winter may reflect recent acquisition of non-gravid forms, degrowth or death of the larger resident cestodes or the selective death of hosts containing larger cestodes. Bush (1990) observed destrobilation in two species of cestodes in willets (*Catoptrophorus semipalmatus*), when the host was in an inappropriate environment for transmission. Degrowth or destrobilation has also been induced in davaineid cestodes by depriving the host of carbohydrate (see Chappell, 1980). Moss and Hanssen (1980) observed a reduction in the nutritional quality of heather, the main food of red grouse, during winter. Consequently, whichever mechanism is responsible, the reduction of per capita cestode mass during winter may reduce the energetic drain of the cestodes at a time of nutritional stress, and thereby benefit both parasite and host. In addition, restricting reproduction to the summer means that *P. urogalli* proglottids are not shed during harsh winter conditions where chances of survival may be low. Unfortunately, in the present study cestodes were not examined to determine if they were destrobilated or newly acquired, and this should be addressed in future research.

Another source of variation in per capita cestode mass in the present study was the number of cestodes present. However, the strength of this relationship varied with age and season, the strongest negative correlation being in young grouse in the summer (Fig. 3). Depression of the weight of individual cestodes has been related to overcrowding in other cestode infections (e.g., the fowl cestode *Raillietina cesticillus*; Read, 1942). Possible explanations for the 'crowding' phenomenon include competition among cestodes for resources or scolex attachment sites, the effects of host immunity and direct inhibition of worm growth by con-specifics (see Avery, 1969; Chappell, 1980). However, the interpretation of these effects in data from natural infections can be confounded by sampling bias (Keymer and Slater, 1987; Shostak and Scott, 1993). Although data from the present study provides some evidence for an intensity dependent effect on the development of *P. urogalli,* larger sample sizes are required for confirmation.

Young grouse weighed significantly less than adults in the summer and carried a greater total biomass of cestodes relative to their bodyweight. If less space is available in the gastro-intestinal tract of younger birds then cestodes may be more likely to be physically ejected from the gut by the exertion of sudden flight, as has been observed in the field (Shipley, 1909; R. J. Delahay, pers. obs.). Such crowding of cestodes in young birds might also result in constraints on cestode growth and could explain the negative relationship between per capita cestode mass and the intensity of infection for young grouse in their first summer. This suggests that anecdotal observations of high cestode intensities in young grouse during the summer, may relate to the combined effects of seasonal changes in the weight of cestodes and the relatively smaller body size of young birds, rather than to differences in cestode intensity alone.

Inter-specific competition between parasites may be an important process in parasite communities (Halvorsen, 1976). There was a significant negative correlation between numbers of *T. tenuis* and total biomass of *P. urogalli* in grouse in the present study. However, this correlation could equally be explained by levels of the two parasites being influenced in opposite directions by a third factor such as host behaviour or environmental conditions. Although the red grouse has been the subject of several mathematical models (e.g., Hudson et al., 1992) attempting to describe the effects of parasites on host population dynamics, only the nematode *T. tenuis* has been considered. It is recommended that future research address the potential for interactions with other intestinal parasites such as *P. urogalli* and *H. microps.*

There was no simple relationship between the abundance of cestodes in grouse and location, as differences between male and female grouse were inconsistent across sites. Wissler and Halvorsen (1977) also found considerable quantitative differences in the distribution of *R. urogalli* between different populations of willow grouse in Norway. The reason for such variation in the present study is unclear.

The present study provides no evidence for an effect of *P. urogalli* on grouse body condition. Neither the abundance nor the total biomass of cestode infections was related to grouse sternum musculature scores. This is consistent with the findings of Thomas (1986) who recorded no effect of cestode parasitism on fat and protein reserves in a Hudson Bay population of willow ptarmigan *Lagopus lagopus albus.* Paradoxically, in the present study the index of comb brightness in cock red grouse was positively correlated with cestode abundance. As comb size and brightness are correlates of social status in red grouse (Moss et al., 1979) one potential explanation for this relationship is that dominance carries a cost that may include susceptibility to parasites (see Moss et al., 1994).

However, the evidence for such a relationship is ambiguous, as comb dimensions were not correlated with cestode abundance or total biomass.

In conclusion, young and old grouse contained similar numbers of *P. urogalli* in summer and winter, although in the summer cestode biomass per unit of grouse bodyweight was greater in young than old grouse. Both total biomass and per capita cestode mass were also significantly greater in the summer. This is likely to reflect a pattern of seasonal reproduction in *P. urogalli* and suggests an important role for young grouse in transmission of this cestode. In young grouse in the summer, there was also evidence for an intensity dependent constraint on cestode growth. Although based on a relatively small sample size, the present study has highlighted several areas of potential importance for future research on the ecology of *P. urogalli* in red grouse.

ACKNOWLEDGMENTS

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