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Parasitized grouse are more vulnerable to predation as revealed by a dog-assisted hunting study

Marja Isomursu[1], Osmo Rätti[2], Pekka Helle[3] & Tuula Hollmén[4]

[1] *Finnish Food Safety Authority Evira, Research Department, Fish and Wildlife Health Research Unit, P.O. Box 517, FI-90101 Oulu, Finland (e-mail: marja.isomursu@evira.fi)*
[2] *Arctic Centre, University of Lapland, P.O. Box 122, FI-96101 Rovaniemi, Finland*
[3] *Finnish Game and Fisheries Research Institute, Oulu Game and Fisheries Research, Tutkijantie 2 E, FI-90570 Oulu, Finland*
[4] *Alaska Sealife Center, 301 Railway Avenue, P.O. Box 1329, Seward, AK 99664, USA*

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Sublethal parasite infections may cause mortality indirectly by exposing the host to predation. Intestinal helminth parasites are common in forest grouse, the capercaillie *Tetrao urogallus*, the black grouse *Tetrao tetrix* and the hazel grouse *Bonasa bonasia*, and these grouse are valuable prey for several species of predators. We evaluated the hypothesis that parasite infection makes the host more vulnerable to predation by comparing the intestinal parasite infection status of grouse hunted with a trained dog to that of grouse hunted without a dog. Cestode infections were more common in grouse hunted with a dog supporting the hypothesis. Cestodes were mostly parasites of juvenile grouse but even among juveniles only, cestodes were more prevalent in dog-assisted hunting bag. The results suggest that mammalian predators could prey more selectively on parasitized individuals and that intestinal parasites may contribute to the high mortality of juvenile grouse through increased predation.

Introduction

The negative influence of parasites on host condition or fecundity can usually be seen, but there is also evidence that parasites may have an indirect effect on mortality by increasing the host's vulnerability to predation (Temple 1987, Hudson *et al*. 1992, Murray *et al*. 1997). Parasites with indirect life-cycles depend on predators, the definitive hosts, to consume the parasite-infected intermediate host (e.g. Rau & Caron 1979, Knudsen *et al*. 2001, Joly & Messier 2004). However, infections of some gastrointestinal parasites are connected to increased susceptibility to predation in red grouse *Lagopus lagopus scoticus* (Hudson *et al*. 1992) and pheasant *Phasianus colchicus* (Millán *et al*. 2002), even though these parasites do not need carnivores to complete their life-cycle and die if their host is consumed.

Parasite-induced predation can alter the host population dynamics. When predators prey selectively on heavily infected individuals, they effectively remove parasites from the host population dampening the direct destabilizing effects of parasites (Dobson & Hudson 1995). On the other hand, parasite-induced predation caused by sublethal parasites may destabilize predator–prey dynamics and cause population cycles even though parasites have no effect on the prey population in the absence of predators (Ives & Murray 1997).

Boreal grouse commonly harbour intestinal nematode and cestode parasites in their small intestine (Isomursu *et al*. 2006). All three forest dwelling species, the capercaillie *Tetrao urogallus*, the black grouse *Tetrao tetrix* and the hazel grouse *Bonasa bonasia*, share essentially the same parasite species in Finland.

Grouse are profitable prey for several mammalian predators. The most important of them in boreal forests is the red fox which can limit the grouse populations especially when alternative prey is scarce (Marcström, Kenward & Engren 1988, Lindström *et al*. 1994, Smedshaug *et al*. 1999). Grouse are also important game birds and they are commonly hunted with the aid of a trained dog that roams ahead of the hunter and reveals the hiding prey by barking or staying and pointing. Without a dog, the hunter walks alone in a suitable grouse habitat and encounters prey more accidentally. The dog presumably locates the prey by the same cues as wild canine predators which is why hunting with a dog can be regarded as close simulation of natural predation (e.g. Hudson *et al*. 1992, Storaas *et al*. 1999).

In the present paper, we evaluate the hypothesis that intestinal parasite infection makes the host more vulnerable to predation. We study hunting bag to reveal a possible association between parasite infection and the two aforementioned hunting methods (with a dog *vs*. without a dog). A specific prediction of the hypothesis is that parasitized grouse are overrepresented in the dog-assisted hunting bag indicating their increased vulnerability to predation.

Material and methods

From 1996–2002, hunters from five Finnish game management districts (Lappi, Oulu, Kainuu, Keski-Suomi and Satakunta) collected intestines from grouse shot during the regular hunting season in autumn from 10 September to 31 October. For each individual, one of the wings was also included to determine species, age (adult or juvenile) and sex (Cramp & Simmons 1980). A total of 1120 samples from which both sex and age could be determined were examined for parasites. To standardize the material for this study, we chose 623 samples that were all shot with a shotgun which requires a closer shooting distance (≤ 40 m) than a rifle. Of these 623, 184 (30%) were capercaillie, 277 (44%) black grouse and 162 (26%) hazel grouse. A dog assisted the hunter in 289 (46%) cases. The most common type of dog was a barking dog, typically Finnish spitz, which was used in 75% of the cases. The proportion of pointers and other breeds was 15% and 10%, respectively.

Samples were frozen in a plastic bag as soon as possible and kept frozen until the examination, when the intestines (including caeca) were dissected and macroscopic helminth parasites were extracted and stored in 10% formalin solution for later identification. Nematodes were individually counted and identified microscopically. Cestodes were dyed with carmine red (Sigma Chemicals) and identified microscopically. Cestodes could not be counted due to the fragmentation of most of the worms.

The associations between host sex, age, species, the month of sampling (September or October), the use of dog and the occurrence of intestinal helminths was studied using hierarchical loglinear modelling with backward elimination procedure ($P = 0.05$) (SPSS programme ver. 11.5). The least useful interactions were dropped from the saturated model step by step until interactions could not be eliminated without significantly impairing the model. This process yielded the most parsimonious well-fitting model. Two different models were studied, one for cestodes (Model 1) and one for nematodes (Model 2). In addition, χ^2-test was used to assess the interactions in detail.

Results

All grouse species harboured one nematode parasite, the ascarid *Ascaridia compar* (prevalence 23.4%) and one species of cestodes, *Skrjabinia* (*Raillietina*) *cesticillus*. Additionally, capercaillie and black grouse had two other species of cestodes, *Paroniella* (*Raillietina*) *urogalli* and *Hymenolepis* sp. All three cestode species were pooled together in the analysis. The most prevalent cestodes in all bird species were *S. cesticil-*

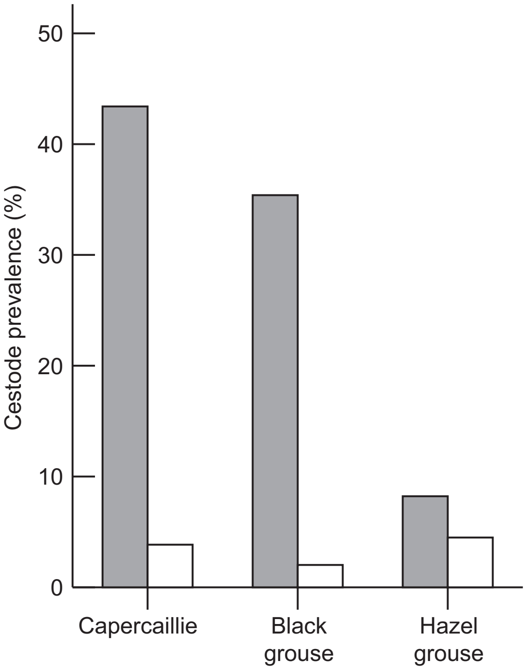

Fig. 1. Prevalence of cestodes by age class and host species. Grey bars = juveniles, white bars = adults.

lus (13.5%) and *P. urogalli* (7.7%), while *Hymenolepis* sp. was found only in 1.4% of the birds. All cestode species infected more often juveniles (32.2%) than adults (3.4%). Instead, females and males were rather equally infected by cestodes (21.2% and 19.0%, respectively).

Hunting with a dog yielded more capercaillie and less hazel grouse but black grouse was the most common species in both bags. Species composition of the dog-assisted bag was 47% black grouse, 41% capercaillie and 12% hazel grouse. Bag hunted without dog had 43% black grouse, 20% capercaillie and 37% hazel grouse.

According to loglinear Model 1 (cestodes) there was a statistically significant interaction between the bird's age, the occurrence of cestodes and bird species (Table 1). Cestodes were much more prevalent in juvenile capercaillie and black grouse than in adults ($\chi^2 = 35.97$, $P < 0.001$; $\chi^2 = 39.45$, $P < 0.001$, respectively) but in hazel grouse cestodes were less common in both age groups and the difference was not statistically significant ($\chi^2 = 0.96$, $P = 0.33$) (Fig. 1). There was also an association between age, month and bird species as the age structure of capercaillie and black grouse bags changed from September to October (Table 1). In the first half of the season, most birds were juvenile (64% of capercaillie, 74% of black grouse), but later, in October, juvenile and adult capercaillie were hunted almost equally (51% juveniles) and a slight majority of black grouse (55%) were adults. Hazel grouse bag, on the other hand, was not juvenile-biased at any time. The sex ratio of the bag was related to the use of dog in two bird species (Table 1). Hunting with a dog yielded more female grouse than without dog in black grouse and hazel grouse bags ($\chi^2 = 5.39$, $P = 0.02$; $\chi^2 = 8.62$, $P = 0.003$; respectively) while in capercaillie there was no significant difference ($\chi^2 = 0.85$, $P = 0.36$).

The occurrence of cestodes was associated with the use of a hunting dog (Table 1). All species of grouse hunted with dog were more frequently infected with cestodes (27%) than grouse hunted without dog (14%) (comparison by bird species in Fig. 2). Also, the prevalence of cestodes was dependent on the month of sampling (Table 1). In the first half of the hunting season in September, the prevalence was 25% but it decreased to 11% in October. Regardless of this, the grouse hunted with a dog had a higher

Table 1. The most parsimonious hierarchical loglinear model of the interactions between the occurrence of cestodes, the use of dog, host species, sex, age and month. The *P* value for the final model indicates the goodness-of-fit of the model and the other *P* values indicate significance of eliminating the interaction from the model.

	Likelihood ratio χ^2	df	Δl.r. χ^2	Δdf	*P*
Final model (step 45):	59.85	67			0.720
Dog × cestodes	66.90	68	7.05	1	0.008
Month × cestodes	70.92	68	11.07	1	0.001
Month × age × species	71.13	69	11.28	2	0.004
Cestodes × age × species	67.17	69	7.32	2	0.026
Dog × species × sex	68.66	69	8.81	2	0.012

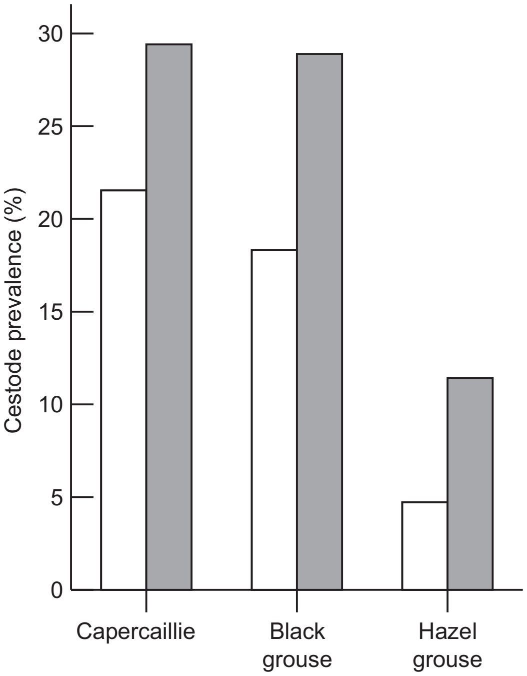

Fig. 2. Prevalence of cestodes in grouse hunted with a dog or without a dog. Grey bars = with dog, white bars = without dog.

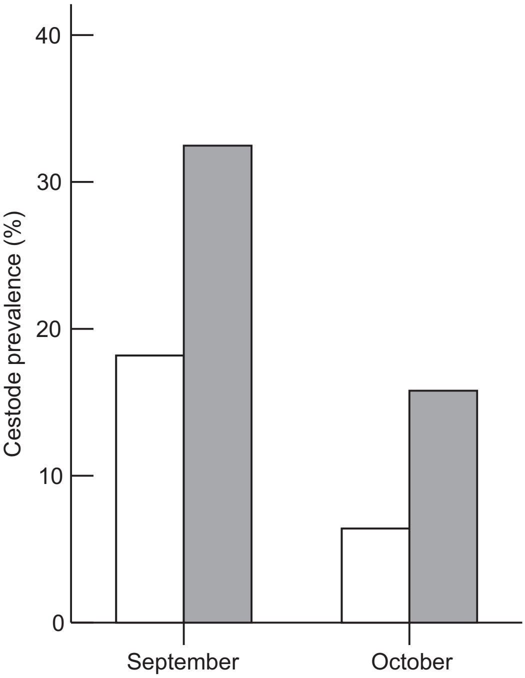

Fig. 3. Prevalence of cestodes in grouse hunted with a dog or without a dog in September and October. All three grouse species are pooled together. Grey bars = with dog, white bars = without dog.

prevalence of cestodes than those hunted without a dog in both months (Fig. 3).

All in all, by October the proportion of juvenile, cestode infected grouse had markedly decreased in the bag. However, the connection between cestode infection and dog-assisted hunting remained. In the juvenile grouse hunted with a dog in October, the prevalence of cestodes was 32% while in juvenile grouse hunted by man alone it was 10%. To be sure that the correlation between cestode infection and the age of grouse does not bias our results we performed hierarchical loglinear analysis by including juvenile individuals only. The interaction between use of dog and cestode infection was still statistically significant (Step 20, Dog × cestodes, deviance = 4.39, df = 1, $P = 0.04$) suggesting that the higher proportion of cestode infected individuals in dog assisted bag was not due to higher susceptibility of juveniles to hunting with dogs as compared with adults.

Model 2 (nematodes) did not produce any statistically significant two- or three-way interactions including the use of dog (Table 2). The interaction between age, month and species was statistically significant in this model as it was in Model 1 (*see* above). In addition, there was an

Table 2. The most parsimonious hierarchical loglinear model of the interactions between the occurrence of nematodes, the use of dog, host species, sex, age and month. The *P* value for the final model indicates the goodness-of-fit of the model and the other *P* values indicate significance of eliminating the interaction from the model.

	Likelihood ratio χ^2	df	Δl.r. χ^2	Δdf	*P*
Final model (step 26):	42.28	39			0.331
Month × sex × nematodes	46.46	40	4.18	1	0.041
Age × month × species	57.06	41	14.78	2	< 0.001
Species × sex × age × dog × nematodes	49.23	41	6.95	2	0.031

interaction between sex, month and occurrence of nematodes because prevalence of nematodes increased in male grouse from September (26%) to October (32%). The statistically significant interaction between five different variables suggests a very complicated association between variables and does not allow a parsimonius interpretation.

Discussion

In all three grouse species, individuals hunted with a dog were more commonly infected with cestodes than those hunted without a dog. Cestodes were mostly parasites of juvenile grouse which is explained by their feeding habits. Chicks feed mainly on invertebrates and also juvenile grouse use more animal food, mainly insects, than adults (Helminen & Viramo 1962, Kastdalen & Wegge 1985). Ants and coleopterans serve as intermediate hosts for grouse cestodes and transmit the infection to young grouse (Reid 1991). Since juvenile grouse were more often infected by cestodes, one may argue that the higher proportion of cestode infected individuals in dog assisted bag results from vulnerability of juveniles to hunting with a dog due to their inexperience. However, our analysis showed that this was not the case as the phenomenon was independent of the age of the bird. Instead, results suggest that cestodes increased vulnerability of grouse to this hunting method.

Hunting with a dog can be regarded as close simulation of natural predation (e.g. Hudson *et al*. 1992, Storaas *et al*. 1999). Thus, our results suggest that parasitized grouse are more likely to be preyed upon by canine predators. Parasitism has also been connected to increased predation in red grouse (Hudson *et al*. 1992), pheasant (Millán *et al*. 2002), moose *Alces alces* (Joly & Messier 2004) and Townsend's voles *Microtus townsendii* (Steen *et al*. 2002), although there are also opposite results in the case of red grouse (Moss *et al*. 1990) and field voles *Microtus agrestis* (Haukisalmi *et al*. 1994).

The simplest proximate reason for parasite-induced predation would be the negative impact of parasitism on host's condition. Predators are often assumed to prey more on "easiest targets", weak or sick individuals. Temple (1987) found that when a prey species is relatively difficult to catch, the predator catches disproportionately substandard, e.g. parasitized, individuals. Normally agile and strong prey animal could be weakened enough by parasites to be caught. Decreased activity is a known consequence of some parasite infections (Poulin 1994). For example, *Echinococcus granulosus* forms larval cysts (hydatid cysts) in the lungs of moose which can affect lung function and make moose more vulnerable to wolf predation (Rau & Caron 1979, Joly & Messier 2004). Concerning the grouse species of this study, we do not have any direct observations or data showing that infected individuals would be in a noticeably poor condition.

Effects of parasites could also make the host more easily detectable. Parasites can induce behavioural changes that make the animal become more conspicuous e.g. by choice of habitat (Moore 2002). Chemical cues are important for canine predators with acute sense of smell. Parasites can sometimes increase the odour of the host, such as in the case of the caecal nematode of red grouse, *Trichostrongylus tenuis*. The parasite can damage caecal function and make the incubating grouse produce more caecal faeces and thus emit more scent. Parasitized red grouse are more often found by a trained dog than grouse with experimentally reduced parasite load (Hudson *et al*. 1992).

The proportion of juvenile grouse decreased in the bag during the hunting season suggesting higher juvenile than adult mortality. The prevalence of cestodes decreased as well from September to October. Therefore, high juvenile mortality may be induced by parasites. Another explanation for decreasing cestode prevalence is that instead of the hosts, the cestodes die during autumn and new infections are not acquired because the use of animal prey decreases rapidly after chick period. By September and October, young grouse are 3–4 months old and the cestodes they acquired as chicks may already be at the end of their life span. Mature worms of *S. cesticillus* start to disintegrate by 70 days post infection (Gray 1972). However, juvenile capercaillie and black grouse use insect prey to some extent even in autumn (Helminen & Viramo

1962, Pulliainen 1979), which exposes them to new cestode infections after chick period.

Interestingly, the proportion of cestode-infected, predominantly juvenile grouse in the dog-assisted bag remained high throughout the season despite the general decrease of cestode prevalence and juvenile proportion. The mortality of juvenile capercaillie and black grouse is known to be high (Lindén 1981) but the effect of parasites on the mortality is unclear. Our findings suggest that high juvenile mortality among these species may be at least partly due to parasite-induced predation.

When trained hunting dogs seem to find more parasitized grouse than human hunters it is tempting to draw a conclusion that also other canine predators catch more parasitized grouse. The consequences of such a phenomenon can be significant for grouse population dynamics. Predation can have a pronounced limiting effect on grouse population density and even drive population fluctuations (Angelstam *et al*. 1985, Marcström *et al*. 1988). The interaction of parasitism of the prey and predation has a further effect and can lead to cyclic fluctuations of both prey and predator population when parasites are sublethal (Ives & Murray 1997). The proximate reasons behind the suggested parasite-induced vulnerability to predation are largely unknown but further studies in parasite-induced changes in the physiology or behaviour of the grouse would shed more light on the matter.

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