

Vector-borne parasites decrease host mobility: A field test of freeze or flee behaviour of willow ptarmigan

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Abstract

Transmission mode has been suggested to be a strong predictor of virulence. According to theory, the transmission of vector-borne parasites should be less dependent on host mobility than directly transmitted parasites. This could select for increased exploitation of host resources in parasites transmitted by vectors, which may be manifested as higher virulence. Here, we test the prediction that there is an association between transmission mode and the effect on host mobility by comparing parasite infection levels and mobility in willow ptarmigan (*Lagopus lagopus* L.). We examined the endoparasite infracommunities of individual hosts to obtain annual, quantitative data on four vector-transmitted species (*Leucocytozoon lovati*, *Trypanosoma avium*, *Haemoproteus mansonii* and microfilaria), two directly transmitted species (*Trichostrongylus tenuis* and *Eimeria* sp.) and two species with indirect life cycles (*Hymenolepis microps* and *Parionella urogalli*). We then used observed variations in freeze-or-flee responses of individual willow ptarmigan to assess whether parasite intensities were related to scored freezing responses. From a field data set covering a period of 9 years from a single area, we found that stronger freezing responses were associated with higher intensities of vector-borne parasites, especially with higher intensities of the haemosporidian *L. lovati*. Freezing responses were not associated with parasites transmitted in other ways. Thus, high intensities of vector-borne parasites tended to reduce host movements, while parasites with other transmission modes did not.

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1. Introduction

Some parasite species are hardly noticeable to their hosts while infection with others is fatal. Our current understanding of this variation in virulence is based on the idea of a trade-off between parasite reproduction and host mortality (Anderson and May, 1982; Ebert and Herre, 1996; Frank, 1996; Gandon et al., 2002). Since a parasite extracts resources from its host, it can only reproduce faster by harming the host more, thus decreasing both host and parasite survival. This trade-off will vary for different kinds of parasites and transmission mode has been suggested to be a strong predictor of virulence (Fine, 1975; Ewald, 1983; Frank, 1996). Ewald (1983) suggested that vector-borne (VB) parasites should pay a smaller cost because they do not depend on host mobility, compared with parasites that need mobile hosts to spread their transmission stages, such as directly transmitted (DT) parasites. VB parasites may

actually derive an advantage from immobilizing their hosts, because this would make the host an easier target for blood-sucking insects (Ewald, 1994). We should therefore expect selection for higher disease severity in VB parasites compared with parasites with other transmission modes. This could also lead to an increased virulence (i.e. parasite-induced host mortality as defined in Anderson and May, 1982) in hosts infected by VB parasites.

Although Ewald's idea appears logically consistent, his hypothesis has recently been criticised because it does not consider the evolutionary effect on DT parasites with reduced transmission potential compared with VB parasites (Day, 2002). If reduced transmission potential leads to reduced lifespan of a DT parasite, this could lead to a selective advantage for higher replication rates and increased virulence. A mathematical analysis suggested that Ewald's hypothesis was only supported under certain conditions (Day, 2002). Alternative explanations for a higher virulence of VB parasites have therefore been suggested, including an increased ability to infect distant individuals in a spatially structured host

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population (Boots and Sasaki, 1999) and a larger inoculum size (Day, 2002). Anyhow, most workers appear to accept that there is a pattern of higher virulence of VB parasites than those that are transmitted in other ways. However, to our knowledge the only empirical evidence for this is based on a comparison of human parasites (Ewald, 1994), which has been criticised because possible confounding variables were not taken into account (Read et al., 1999).

Currently Ewald's hypothesis is therefore questioned, both for its theoretical ambiguity and for lack of empirical evidence. To address this critique it is important to keep in mind that Ewald based his idea on two main assumptions: (i) that the cost of affecting host mobility is smaller for VB parasites than for parasites with other transmission routes; and (ii) that there is a relationship between the parasite's effect on host mobility and its virulence. Day's (2002) analysis is mainly based on the second assumption but the fundamental part of Ewald's hypothesis is in the first assumption. A first logical step in testing the hypothesis is therefore to look for empirical evidence for a relationship between host mobility and transmission mode.

If VB parasites have, in general, a stronger effect on host mobility than DT parasites, we would expect to find a consistent pattern between transmission mode and mobility within a host population that harbors both kinds of parasites. Here, we explore this idea using observed variations in freeze or flee behaviour of willow ptarmigan (*Lagopus lagopus*) as a model. The typical response in *Lagopus* spp. to an approaching threat is to crouch and remain still, relying on their camouflage to protect them from being spotted (Watson and Jenkins, 1964; White and Weeden, 1966; de Juana, 1994; unpublished observations). At some point the approaching predator comes within a critical distance and the bird flees rapidly. This behaviour is observed in a wide range of species, from marine crustaceans to large mammals and individuals within a group of prey may often show marked behavioural differences—some will rapidly flee while others rely on their camouflage and freeze for a much longer time (Fentress, 1968; Smith, 1991). One reason for this variation could be that the cost of fleeing is considerably higher for an infected individual that needs to conserve its energy resources than for a healthy one. Prey species infected with parasites affecting host mobility should therefore take larger risks when confronted with a predator and show less willingness to flee.

Willow ptarmigan is infected with a variety of different parasites, some of which are VB while others are transmitted by immobile eggs or larvae (Holmstad et al., 2005). When threatened by approaching hunters during walk up shooting, a group of willow ptarmigan often show large variation in individual flushing distances; some may flush well out of range, while others are more reluctant to leave their hideouts and remain still at the flush site. We collected the birds through walk up shooting (i.e. unaided by dogs) and examined them for eukaryotic endoparasites. According to the hypothesis of Ewald (1983), we expected that the degree of freezing should be more positively correlated with the infection levels of VB

parasites compared with the levels of parasites transmitted in other ways.

2. Materials and methods

The study area, Nordre Kattfjord, is situated on the island Kvaløya off the North Norwegian coast (69°40'N, 18°15'E). A total of 515 willow ptarmigan were collected during the first 2 weeks of hunting (10–22 September) during the years 1994–2002. These included 312 juvenile and 203 adult willow ptarmigan. All birds were shot during walk up shooting, where hunters actively seek out places where they expect to find willow ptarmigan. Pointing dogs were not used. Since, the mottled brown plumage patterns of ptarmigan provide excellent camouflage and the birds generally remain motionless in proximity of the hunter, they are rarely spotted on the ground and the hunter relies on experience in order to flush them from their hideouts. Accompanying hunters position themselves strategically, such that willow ptarmigan flushed out of shotgun range by one hunter may fly towards and get shot by an accompanying hunter that did not interfere during the initial flushing of birds. For every willow ptarmigan shot flushing distance was scored by a rank scale ranging from 1 to 4. The ranks were 1, flushed out of shotgun range (> 35 m) but shot by accompanying hunter; 2, flushed within shotgun range (15–35 m); 3, flushed at close range (0–15 m); 4, 'sticky' birds flushed and shot, or shot on the ground, while remaining on flush site after the other brood or flock members had flushed.

Birds were classified as either juveniles (2–3-month-old) or adults (older than 14 months) from molting sequence and pigmentation of the primaries (Steen, 1989). Sex was determined from an inspection of gonads. Body mass was estimated as total weight minus weight of the crop contents (± 0.1 g). Endoparasites were examined and quantified following the procedures described by Holmstad and Skorping (1998) and Holmstad et al. (2003).

All statistics were performed using R version 2.1.1 (R Development Core Team, 2005. URL <http://www.r-project.org> ISBN 3-900051-07-0, Vienna, Austria). To examine which factors were associated with the freezing behaviour of *L. lagopus* we used ordinal logistic regression (McCullough and Nelder, 1989) by using the *polr* function from the MASS library (Agresti, 2002; Venables and Ripley, 2002). We ran proportional-odds logistic regressions since the response variable is ordinal and there is a dependency between scores, e.g. a bird having freezing score 4 must have gone through scores 1–3 before reaching score 4. The predictor variables in our model were: Year, Age, Sex and Body mass, four vector transmitted parasites: *Leucocytozoon lovati*, *Trypanosoma avium*, microfilaria (species not identified) and *Haemoproteus mansoni*, two directly transmitted species: *Eimeria* sp. and *Trichostrongylus tenuis*, and two species using non-vector intermediate hosts: *Hymenolepis microps* and *Parionella urogalli*. The potential of each parasite species in explaining the variability in freezing behaviour was explored by testing each parasite separately against a null model without parasites. To control for possible effects of the non-parasite

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