



Research article

Exploration of the epidemiological consequences of resistance to gastro-intestinal parasitism and grazing management of sheep through a mathematical model

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ABSTRACT

Predicting the impacts of selection for decreased faecal egg count (*FEC*) (i.e. host resistance) in grazing ruminants is difficult, due to complex interactions between parasite epidemiology, management and host responses. A mathematical model including heritable between lamb variation in host–parasite interactions, *Teladorsagia circumcincta* epidemiology and anthelmintic drenching, was developed and used to (i) address such interactions and their impact on outcomes including *FEC*, live weight (*LW*, kg) and pasture larval contamination (*PC*, larvae/kg DM), and (ii) investigate how grazing management strategies, aimed at reducing host exposure to infective larvae via pasture moves at 40 day intervals, affect these outcomes. A population of 10,000 lambs was simulated and resultant *FEC* predictions used to assign the 1,000 lambs with the highest and lowest predicted *FEC* to ‘susceptible’ (*S*) and ‘resistant’, (*R*) groups, respectively. The predicted average *FEC* of the *S* group was ~8.5-fold higher than the *R* group across a grazing season. The *R* and *S* groups were then simulated to graze separate pastures (**R_{sep}** and **S_{sep}**); and repeated for 3 grazing seasons to allow predictions to diverge and stabilize. Further, different grazing strategies were superimposed on all groups. *PC* and average *FEC* were affected by whether lambs of different resistance genotype grazed together or separately, with differences increasing across grazing seasons. By the third grazing season the average *PC* of the **R_{sep}** group was reduced by ~83%, and the **S_{sep}** group was increased by ~240%, in comparison to the whole population average. Average *FEC* of the **R_{sep}** group was reduced by ~40%, and the **S_{sep}** group increased by ~46% in comparison to the *R* and *S* groups, respectively, whilst drenching had little impact on the proportional differences in *FEC* between groups. Predicted *LW* was similar for the *R* and **R_{sep}** groups irrespective of anthelmintic treatment, whilst *LW* of the **S_{sep}** group was reduced by ~14% compared to the *S* group for un-drenched lambs, and by ~4% for drenched lambs. The differing grazing strategies were predicted to have little impact on *FEC* or *LW*, with the exception of the **S_{sep}** group which was predicted to have a 2 kg increase in *LW* when drenched and moved to a clean pasture. Together, these results suggest that host genotype has a substantial impact on parasite epidemiology, however the benefits of anthelmintic treatment and grazing management should only be expected for susceptible animals. This supports the use of targeted selective treatment, focussing on susceptible animals.

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1. Introduction

Gastro-intestinal parasitism is one of the most pervasive challenges to the health and welfare of ruminants, causing significant production losses for the sheep industry (Nieuwhof and Bishop, 2005). Effective control of nematode infections relies heavily on the use of antiparasitic drugs; however, reduced efficacy due to the evolution of drug resistance by parasite populations (Jackson and Coop, 2000; Bartley et al., 2003) has stimulated the search for alternative sustainable control methods. Selection for increased host resistance to gastro-intestinal parasitism has previously been proposed as an alternative or complementary control strategy, and is supported by evidence of heritable variation in faecal egg count (FEC) (Bishop and Morris, 2007) and by results of selection in practice (Kemper et al., 2010). However, the benefits of such a strategy seem to depend on management practices (Vagenas et al., 2007).

Although selection for resistance may be viewed as beneficial, predicting the actual benefits of selection for resistance in grazing ruminants can be difficult, due to complex interactions between parasite epidemiology (including host population infection dynamics), management practices including grazing, and host resistance to nematode infections (Bishop and Stear, 1997). Further, the combination of selection for resistance and other control methods, such as grazing management, may provide further complementary benefits and lead to reduced anthelmintic use (Coop and Kyriazakis, 2001). For example, a mixed population may benefit from grazing with animals selected for resistance, whilst grazing selected animals separately may be used to provide pastures with reduced larval contamination. However, resistance of parasites to pharmaceuticals has reduced the effectiveness of grazing management, which is further complicated by the availability of truly clean pasture (Waller, 2006).

Exploring these complex interactions experimentally and determining the benefits of control methods separately or in combination can be costly and time consuming. When using an appropriate mathematical model such constraints can be considerably reduced. As such, the mathematical model of Laurenson et al. (in press) which includes heritable between-animal variation in host-parasite interactions, the epidemiology of *Teladorsagia circumcincta* and anthelmintic drenching protocols, is a tool which may be used to gain insight into the interactions between host resistance, grazing management and parasite epidemiology. Here we use this mathematical model to quantify these interactions between host genotype, control interventions and disease epidemiology. Specifically, we explore the epidemiological consequences of grazing animals with differing genotype for resistance under contrasting drenching protocols. The question being addressed is to what extent does pasture contamination change when grazed by sheep of contrasting genotypes for resistance, as assessed by grazing susceptible and resistant sheep together and apart, and are these differences influenced by anthelmintic treatments. Further, we explore the impact of alternative grazing strategies, aimed at reducing host exposure to infective larvae, on the genetic and epidemiological effects.

Specifically, we explore the impact of set grazing vs. movement onto lightly contaminated or clean pastures, and the impact that such movements have on parasite burden and growth rate.

2. Materials and methods

The mathematical model of Laurenson et al. (2011, in press) which includes heritable between-lamb variation in host-parasite interactions, the epidemiology of *Teladorsagia circumcincta* and anthelmintic drenching protocols, was used as the basis of addressing the interaction between host resistance genotype and parasite epidemiology. A brief description of this model is given below.

2.1. Individual lamb model

A schematic diagram describing the structure of the individual lamb model is provided in Fig. 1. Briefly, in the model a growing lamb is assumed to attempt to ingest sufficient nutrients to meet requirements for growth and maintenance, as defined by its genotype. However, infection with gastrointestinal parasites is expected to result in endogenous protein loss (a function of larval challenge and worm burden), and consequently the lamb invests resources in an immune response to counteract this. Further, components of the host response (e.g., cytokines, gastrin) are associated with a reduction in food intake (Fox et al., 1989; Greer et al., 2005; Kyriazakis, 2010), commonly known as (parasite-induced) anorexia. The combination of protein loss due to parasitism, resource investment in immunity and anorexia results in a lamb acquiring insufficient nutrient resources to fulfil all its requirements for maintenance and optimal growth. Thus, ingested resources, after losses due to parasitism, are assumed to be first allocated to meet the maintenance requirements and remaining resources to be allocated towards growth and immunity proportional to requirements (Kahn et al., 2000; Doeschl-Wilson et al., 2008).

2.2. Population model

Individual animals are simulated within a pre-defined population structure, with between-animal variation assumed to occur for the animal growth attributes, such as maximum growth rate and body composition, maintenance requirements, and immune response to gastrointestinal parasites. Initial input parameters involved in these functions are assumed to be normally distributed, thus distributions such as the over-dispersion of faecal egg count (FEC) described by Bishop and Stear (1997) occur as a consequence of the functions that underlie the model rather than as a result of direct input. All traits, other than those associated with immune acquisition, are assumed to be uncorrelated (Doeschl-Wilson et al., 2008). Traits associated with immune acquisition are assumed to be a function of overlapping effector mechanisms (components of the Th2 immune response) (Jenkins and Allen, 2010), and as such strongly genetically and phenotypically correlated ($r = +0.5$). Further, random environmental variation in daily food intake is assumed to reflect the influence of

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