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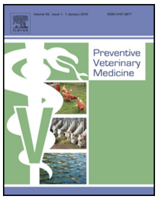

An elaborated SIR model for haemonchosis in sheep in South Africa under a targeted selective anthelmintic treatment regime

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ABSTRACT

Infection with the abomasal nematode *Haemonchus contortus* is responsible for considerable production loss in small ruminants globally, and especially in warm, summer-rainfall regions. Previous attempts to predict infection levels have followed the traditional framework for macroparasite models, *i.e.* tracking parasite population sizes as a function of host and climatic factors. Targeted treatment strategies, in which patho-physiological indices are used to identify the individuals most affected by parasites, could provide a foundation for alternative, incidence-based epidemiological models. In this paper, an elaboration of the classic susceptible-infected-recovered (SIR) model framework for microparasites was adapted to haemonchosis and used to predict disease in Merino sheep on a commercial farm in South Africa. Incidence was monitored over a single grazing season using the FAMACHA scoring system for conjunctival mucosal coloration, which indicates high burdens of *H. contortus*, and used to fit the model by estimating transmission parameters. The model predicted force of infection (FOI) between sequential FAMACHA monitoring events in groups of dry, pregnant and lactating ewes, and related FOI to factors including climate (temperature, rainfall and rainfall entropy), using a random effects model with reproductive status group as the cluster variable. Temperature and rainfall in the seven days prior to monitoring significantly predicted the interval FOI ($p \leq 0.002$), while rainfall entropy did not ($p = 0.289$). Differences across the three groups accounted for approximately 90% of the variability in the interval FOI over the period of investigation. Maintained FOI during targeted treatment of cases of haemonchosis suggests strong underlying transmission from sub-clinically infected animals, and/or limited impact on pre-existing pasture contamination by removal of clinical worm burdens later in the grazing season. The model has the potential to contribute to the sustainable management of *H. contortus* by predicting periods of heightened risk, and hence to focus and optimise limited resources for monitoring and treatment. SIR-type model frameworks are an alternative to classic abundance-based compartmental models of macroparasite epidemiology, and could be useful where incidence data are available. Significant challenges remain, however, in the ability to calibrate such models to field data at spatial and temporal scales that are useful for decision support at farm level.

1. Introduction

The advent of a globally extensive and intractable problem of anthelmintic resistance (AR) in small ruminants (Waller, 1997; Papadopoulos et al., 2012; Torres-Acosta et al., 2012) has prompted a paradigm shift in anthelmintic-based control of parasites (Morgan et al., 2013). The conventional practice of treating the whole flock on a regular basis, either routinely or in response to observed effects of worm infection, is recognised as no longer sustainable. Rather, current recommendations point to a sustainable integrated parasite management (***s***IPM) approach (Van Wyk et al., 2006), mainly involving targeted selective treatment (TST) and targeted treatment (TT) strategies (Bath and Van Wyk, 2009; Charlier et al., 2014). However, to date the uptake of TST and TT strategies by farmers has been slow, despite calls for their adoption (Van Wyk et al., 2006; Besier, 2012) in the interests of a sustainable, profitable and eco-friendly small ruminant industry (Fitzpatrick, 2013). The limited uptake has been attributed mainly to implementation complexity and labour demands associated with application of TST and TT

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strategies, in the face of conflicting advocacy for their implementation (Bath, 2006; Besier, 2012).

The FAMACHA system (Malan and Van Wyk, 1992; Bath et al., 1996; Malan et al., 2001; Van Wyk and Bath, 2002), developed in South Africa and widely validated (Kaplan et al., 2004; Vanimisetti et al., 2004; Mahieu et al., 2007; Van Wyk, 2008; Molento et al., 2009; Reynecke et al., 2011), is a field-based test that uses rank colour scores (1–5) to grade levels of anaemia, assessed from the conjunctival membrane with the help of a standardised colour chart. FAMACHA-based TST strategy aims to retain an effective proportion of parasites in refugia, *i.e.* unexposed to anthelmintic treatment, by enabling detection and subsequent treatment of only those individual animals in a flock that are unable to manage their current worm burden unaided (Van Wyk, 2001), as opposed to the conventional approach of whole-flock treatment when parasitosis is detected, or high treatment frequency as a preventive strategy (Van Wyk et al., 2006). Parasites in refugia dilute, through breeding, resistant parasite genotypes and delay the propagation of AR.

FAMACHA-based TST can achieve good control of haemonchosis in sheep, but is labour-intensive, with weekly checks of individual animals recommended during the transmission season (Van Wyk and Bath, 2002). The transmission of *Haemonchus contortus* is strongly influenced by the weather, particularly effects of rainfall, temperature and sunlight on larval availability (O'Connor et al., 2007a, 2007b; Van Dijk et al., 2009; Van Dijk and Morgan, 2011; Khadijah et al., 2013; Wang et al., 2014), and by husbandry factors that determine exposure to infective larvae (Morley and Donald, 1980; Van Wyk, 2001; Parker et al., 2010). It ought, therefore, to be possible to predict periods of heightened risk, and tailor intensity of monitoring accordingly. This paper makes such an attempt, using a novel modelling approach.

Models of macroparasite dynamics traditionally track population abundance, applying understanding of the effects of climatic and other factors on transmission through parameters representing vital rates such as development and survival (Smith and Grenfell, 1994; Cornell, 2005; Rose et al., 2015). This approach is limited by imperfect mechanistic understanding of transmission, especially in field situations different from those used to parameterise the models, and the high resolution of data needed on stock movements and local conditions experienced by free-living parasite stages. Model parameters can be inferred by fitting them to observed parasite abundance data, but this requires longitudinal field data on parasite abundance, which are rarely available (Smith and Grenfell, 1994). Increased implementation of TST provides an opportunity to apply a SIR (susceptible-infected-recovered) type model framework, more usually applied to the incidence of infectious (microparasitic) disease (Kermack and McKendrick, 1927; Anderson and May, 1985, 1992), to nematode infections. Thus, the state of individuals changes over time, depending on force of infection and other parameters, with the infected state defined as a high nematode burden detected in the field by TST selection criteria (in this case high FAMACHA scores). This approach makes the assumption that transmission in the population is driven mainly by heavily infected individuals, removing the need to track average parasite burden explicitly, and acknowledging the uneven distribution of parasites among individual hosts (Shaw et al., 1998). The influence of factors such as climate and management on transmission is inferred from the incidence of cases (=high scores), such that their effects are integrated without making the model dependent on specifically parameterised relationships with, for example, parasite vital rates. SIR models have not previously been applied to nematode infections in farmed animals, and this paper aims to assess its feasibility. A successful model could guide the optimisation of TST protocols, especially to match monitoring effort and intervention thresholds to transmission risk.

2. Material and methods

2.1. Study farm

The farm was located on the Highveld and populated with an average of 150 Merino ewes for wool production, on approximately 100 ha of grazing land. Ewes grazed separately in groups according to reproductive status (dry, pregnant and lactating). Lambing occurred in synchronised groups in April, August or December in a common paddock containing irrigated Kikuyu (*Pennisetum clandestinum*) pasture; other paddocks were unirrigated natural veldt (Acocks, 1988). After lambing, ewes remained on the irrigated pasture for about three months (90 days). The irrigated pasture was then rehabilitated for a maximum of one month before the next group of highly pregnant ewes was introduced. Movement of ewes between the grass veldt paddocks was determined by herbage availability. Replacement ewes were from a single source outside the farm, mostly as pregnant healthy ewes and deaths and culling constituted 20% of ewes per annum. Weaned lambs were moved off the farm for meat production and were therefore not included in the model. Control of *H. contortus*, the predominant worm species on the farm, was based on weekly FAMACHA evaluation of all animals on the farm, with treatment of diagnosed cases ($\geq$3 FAMACHA score) using levamisole (Ripercol-L, Bayer Animal Health) at 7.5 mg kg^{-1}, previously shown to be effective on this farm.

2.2. Model structure

The basic SIR model framework (Kermack and McKendrick, 1927) was extended to take account of the epidemiology of haemonchosis in a TST setting. Thus, individual ewes were assigned into categories: S (susceptible to infection), E (exposed and infected, but not yet infectious), I (infectious, *i.e.* infected with adult worms and shedding parasite eggs, but not yet diagnosed), D (infectious, and diagnosed by FAMACHA evaluation as cases), P (protected, *i.e.* previously infectious and subsequently having acquired active immunity through infection with *H. contortus*), and R (recovered, *i.e.* earlier diagnosed as cases and subsequently recovered after treatment). Distinguishing between P and R compartments was necessary because in a TST system not all infected animals are treated, only those diagnosed with parasite-associated disease. The abbreviation **S**E**I**DP**R**S was used for the model, as an expansion of the basic SIR formulation.

The infectious period for the infectious state in diagnosed cases ($\geq$3 FAMACHA score) was assumed to be equal to the average interval between FAMACHA evaluations plus the time between treatment and maximum drug effectiveness against *H. contortus*. Ewes that became infectious but did not develop clinical signs (and were therefore not diagnosed or treated) were assumed to be infectious for the duration it takes to acquire immunity (Smith, 2001). Recovered ewes became susceptible to re-infection after waning of the very short indirect residual effect of the levamisole drug, while those with acquired immunity became susceptible to re-infection after immunity had lapsed. This lapse of immunity is an important property for a nematode model, since reinfection at high levels is quite possible even in previously exposed animals. Time for lapse of immunity is a fitted parameter in the model, constrained to 30–90 days. Most ewes will actually be infected and shedding low numbers of eggs most of the time, but cases are defined not as individuals infected *per se*, but only those infected at a high level and therefore clinically affected. Likewise, the immune state is deemed to confer protection against a return to clinical disease as a result of high infection levels, rather than absolute immunity. This captures the partial and transient nature of immunity to *H. contortus*, and to nematode infections in general.