Veterinary Parasitology 255 (2018) 83–90

Contents lists available at ScienceDirect

Veterinary Parasitology

journal homepage: www.elsevier.com/locate/vetpar

Research paper

A climate-driven model for the dynamics of the free-living stages of *Cooperia oncophora*

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ARTICLE INFO

Keywords:
Cooperia oncophora
Nematode
Cattle
Free-living
Model

ABSTRACT

Experimental results and published literature data regarding the development, survival and herbage translocation of *Cooperia oncophora* larvae were used to develop a climate-driven model to simulate the dynamics of the free-living stages. From daily maximum and minimum temperature the model estimated hourly development and survival rates of the pre-infective stages and daily survival of infective third stage larvae (L3) inside the faecal pat and in the herbage. In addition, daily rainfall data were used to calculate the translocation rate of the L3 from the faecal pat into the herbage. The model produced results for the development and survival of the free-living stages that were comparable to previous observations. Temperatures below 6 °C or above 35 °C resulted in a low estimate of developed L3, which in between increased and peaked at an optimal temperature estimate of 25.6 °C. Provided sufficient rainfall the model predicted that the developed L3 would be able to translocate from the faecal pat into the herbage. When validating model output for the herbage contamination with *C. oncophora* infective stage larvae against results of a two year field experiment, the comparison indicated that the model was able to reproduce the observed contamination pattern. Further, detailed examination of different model components helped to identify possible factors causing the decay of larval herbage contamination during winter-spring as occurred in the field experiment.

1. Introduction

Nematode parasites are an important production limiting factor in cattle farming throughout the world (Charlier et al., 2009; Charlier et al., 2014). In New Zealand, one of the most important parasite species infecting cattle is *Cooperia oncophora*. Although this nematode is generally regarded as being less pathogenic than other species (Coop et al., 1979; Herlich, 1965), resistance to the macrocyclic lactone anthelmintics, and to a lesser extent the benzimidazoles, is extremely common in New Zealand (Leathwick and Miller, 2013; Waghorn et al., 2006). Hence anthelmintic-based control of this parasite is often sub-optimal (Leathwick and Miller, 2013) and it is the predominant species in cattle under about 18 months of age. Given the nature of most cattle farming operations in New Zealand today, effective control of *C. oncophora* is largely dependent on the efficacy of levamisole and so the development of resistance to this anthelmintic would likely result in control becoming much more difficult, if not impossible, in many cases.

The management of anthelmintic resistance, and of parasites in the absence of anthelmintic use, can be enhanced by an understanding of the population dynamics of the parasites via implementation of revised control strategies (Barger, 1999). However, relatively little is known of the detailed biology of *Cooperia* spp., and much of this comes from laboratory experiments (Boag and Thomas, 1985; Ciordia and Bizzell, 1963; Rose, 1963) which on their own are often of limited direct application in the field. Building models offers the opportunity to integrate laboratory based data sets in a format which can be applied in the field, assuming that model performance can be validated against suitable field data sets. Previous models have been especially useful in understanding the selection and management of anthelmintic resistance (Barnes et al., 1995; Leathwick, 2012; Leathwick et al., 2012). A recent review of models for gastrointestinal nematodes in ruminants (Verschave et al., 2016a) indicated that currently no species-specific model for Cooperia is available, however, first steps towards a model for the parasitic phase have been published (Verschave et al., 2016b). The aim of this study, therefore, was to enhance our understanding of the dynamics of *C. oncophora* by integrating all current knowledge into a deterministic climate-driven model for the free-living stages, and testing model outputs against an independent field data set.

2. Materials and methods

Data collected from a comprehensive review of relevant scientific

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https://doi.org/10.1016/j.vetpar.2018.03.026
Received 1 October 2017; Received in revised form 28 March 2018; Accepted 29 March 2018

literature was combined with previously unpublished data (Sauermann, 2014) to form the basis of the model. Data from a large scale field study on the production costs of failing to control *C. oncophora* infections (Candy et al., 2018) was then used to validate the model.

2.1. Laboratory experiments

2.1.1. Development under constant temperatures

Details of the laboratory experiments can be found in Sauermann (2014). Briefly, faeces was collected from three calves, each naturally infected with a mono-specific infection of *C. oncophora*. Subsamples (30 g) were mixed with vermiculite and cultured at constant temperatures of 8, 16, 20, 24, 28 or 32 °C. Third stage infective larvae (L3) were recovered by Baermannisation and enumerated at different times, with shorter intervals at higher temperatures, e.g. every second week at 8 °C but every second day at 32 °C. In order to estimate model parameters the median development time and the maximum number of successfully developed eggs were each averaged across the individual calf samples.

2.1.2. L3 survival under constant temperatures

Similar to the above, individual faecal samples were collected from five calves, mixed with vermiculite and incubated at 25–27 °C for 14 days and the larvae recovered using Baermann funnels (Sauermann, 2014). The recovered larvae were then stored in deionised water, which had shown to be the best available storage medium, in a 24 well plate at 8, 16, 20, 24, 28 and 37 °C, with three replicates of each, for each animal (i.e. 6 temperatures × 3 replicates × 5 calves). At intervals the number of living larvae was determined, by counting the number of larvae reacting to the touch with a soft probe or freely moving. Larvae which remained immobile and didn't respond when probed were assumed to be dead. For determining model parameters in the current work the median survival time was averaged across the individual calf samples.

2.2. The model

To simulate the free-living phase of *C. oncophora* the model separately calculates the development and survival of the pre-infective stages (egg, first and second stage larvae), the survival of the infective (L3) stage and the migration of L3 from the faecal pat onto the herbage. All of these processes are driven by weather data (see below). The development of the egg, first and second larval stages is modelled as a single process, i.e. without differentiation of individual pre-infective stages, because none of the available experimental data differentiated between these stages. Two rate functions describe the progression of individuals through the pre-infective stages to L3, a development rate and a survival rate. The dynamics of the L3 is described by a survival rate, the rate of migration of individuals from the faecal pat onto the herbage and the rate of removal of L3 from the population by ingestion of larvae with herbage by grazing livestock. Unless otherwise stated all rates are limited between 0 (zero) and 1 (one).

The model is constructed using the escalator boxcar train method described by de Roos (1988) and de Roos et al. (1992) implemented in Excel (2013, Microsoft Corp., WA, USA). The box-car train approach represents life history stages as an array (a series of cells) which collectively record the number of individuals present in that stage. Individuals enter the array (e.g. as eggs) and progress from cell to cell as they age (e.g to L1 and L2) at a rate determined, in this case, by temperature and moisture. Once they leave the last cell they transfer to the next life-history stage (e.g. L3). This format has a number of advantages, including its simplicity, capacity to model populations with continuous recruitment and overlapping generations and that it results in an approximately normal distribution of development/survival times (De Wit and Goudriaan et al., 1974). It is also amenable to model building using common software packages such as Microsoft Excel which makes it highly transferable and accessible to a wide range of end-users. Previous applications of this approach can be found in Leathwick (2013), Leathwick et al. (2015), Leathwick et al. (2016) and Leathwick et al (2017).

2.2.1. Development of the pre-infective stages

In cattle faecal pats the development of eggs to the infective stage is primarily dependent on temperature. This is because soil moisture content, along with rainfall and dew, is normally sufficient to prevent full desiccation of the pat before development to L3 is completed (Rose, 1961; Rossanigo and Gruner, 1994). This is especially likely under New Zealand's moist temperate climate (Reynecke et al., 2011).

The survival of pre-infective stages is likely to be strongly influenced by the temperatures to which developing larvae are exposed, even if the interval of exposure may be short, e.g. a temperature of > 40 °C can be lethal in only a few hours (Ciordia and Bizzell, 1963). Incorporating these temperature fluctuations into models can significantly influence predicted survival compared to using daily means (Leathwick, 2013). Therefore, in this model the development of the pre-infective stages was calculated on an hourly time step with hourly temperatures estimated by fitting a sine curve to the recorded daily maximum and minimum temperatures.

To estimate the development rate (Fig. 1) of the pre-infective stages, data from Sauermann (2014) was combined with that of Ciordia and Bizzell (1963), Rose (1963) and Isenstein (1963). The median development time, i.e. the time for 50% of the individuals to reach L3 stage, for each constant temperature was calculated and the reciprocal of the median development times was then regressed against temperature using a logistic function:

$$d_t = a + (b - a) / (1 + \exp((temp - c) / d)) \quad (1)$$

where d_t is the development rate, *temp* is the temperature in degrees Celsius and a to d are regression coefficients (Table 1).

2.2.2. Pre-L3 survival rate

Whereas the development rate defines the speed the individuals move through the pre infective stages and complete their development to the L3, the survival rate defines the developmental success, which is the proportion of individuals successfully progressing from the egg to the L3. To estimate this, the proportion of eggs which successfully developed to L3 at any given temperature, raised to the power of the reciprocal hours required to reach the maximum L3 numbers (Leathwick, 2013) was calculated. To estimate the survival rate (Fig. 1) the data from Sauermann (2014) was combined with data from Ciordia and Bizzell (1963) and the results then regressed against temperature using a concave asymptotic model:

$$s_t = a - b \times \exp(c \times temp) \quad (2)$$

Where s_t is the survival rate, *temp* is the temperature in degrees Celsius and a to c are regression coefficients (Table 1). However, once the temperature exceeds 40 °C this function will produce negative values and was therefore limited to a minimum of zero. This effectively means that developing stages die rapidly at temperatures greater than 40 °C.

2.2.3. L3 survival in herbage and faeces

The infective third stage remains enclosed in the sheath of the second stage larvae, which explains their resilience towards a wide range of climate conditions. However, as these larvae are non-feeding they rely on stored reserves, acquired during the previous stages, as their sole energy source. The utilization of energy is dependent on the metabolic rate, which is highly correlated with ambient temperature, and once the energy reserve is depleted the L3 is unable to establish in a host even if ingested and soon dies (Eckert, 1967). On this basis, we follow Leathwick et al. (2015) and model L3 survival as an aging process driven by temperature (Fig. 1). Thus, newly formed L3 enter the first boxcar and progress through the cells at a rate determined by