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Short communication

Modelling *Cooperia oncophora*: Quantification of key parameters in the parasitic phase

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ABSTRACT

Cooperia oncophora is one of the most common intestinal nematodes in cattle. It is also the dose-limiting species for the most frequently used anthelmintics, and consequently, the species usually involved in reports of anthelmintic resistance. However, little information is available on its population dynamics, hindering the parameterisation of transmission models to support understanding of the impact of anthelmintic resistance, climate change and alternative control strategies on nematode epidemiology. This systematic review and meta-analysis provides estimates for key life history traits of the parasitic phase of *C. oncophora* and investigates potential influences of acquired immunity on these traits.

Mathematical models that simulate transmission dynamics of gastro-intestinal nematode infections have already been around for several decades in the field of veterinary parasitology (e.g. Gordon et al., 1970; Gettinby et al., 1979; Grenfell et al., 1987; Barnes and Dobson, 1990). Given the variety of factors influencing gastro-intestinal nematode infections (e.g. climate, parasite-host interactions) such models can be essential tools to represent and manipulate such systems in ways that would not be possible or practical in the field (Scott and Smith, 1994). In the coming decades, parasitic disease patterns are expected to change due to the impact of climate change and the growing issue of anthelmintic resistance (van Dijk et al., 2010). The nature and impact of these changes, however, is difficult to foresee. Parasite transmission models enable the extrapolation of current knowledge to alternative scenarios and can therefore enhance our understanding of parasite epidemiology under changing conditions (Rose et al., 2015). Moreover, they play an important role in obtaining insights in the development of anthelmintic resistance (Gettinby et al., 1989; Barnes and Dobson, 1990) and underpin the search for alternative control strategies (Smith et al., 1987; Charlier et al., 2014). Because of its high prevalence and pathogenicity, *Ostertagia ostertagi* has been the primary focus of transmission models developed to simulate gastro-intestinal nematode infections in cattle (Gettinby et al., 1979; Grenfell et al., 1987; Chaparro et al., 2013; Rose et al., 2015). Key life history traits of the parasitic phase of *O. ostertagi* were recently quantified through meta-analysis to facilitate the development and parameterisation of future transmission models (Verschave et al., 2014). However, in the light of the development of anthelmintic resistance, *Cooperia oncophora*, another highly abundant nematode of cattle, gains impact as a dose-limiting species for the most commonly used anthelmintics (Sutherland and Leathwick, 2011). Despite its growing importance, no transmission model for this nematode species has been developed yet. Moreover, little information is available on the population dynamics of *C. oncophora*, which is crucial for the development and parameterisation of specific nematode transmission models. Here, we provide the results of a systematic review and meta-analysis that quantifies the main life history traits of the parasitic phase of *C. oncophora* and investigates potential influences of immunity on these traits.

The four life history traits of the parasitic phase of *C. oncophora* addressed were: (1) the pre-adult mortality, (2) the adult mortality, (3) the hypobiosis factor and (4) the female fecundity. The pre-adult and adult mortality are respectively defined as the instantaneous

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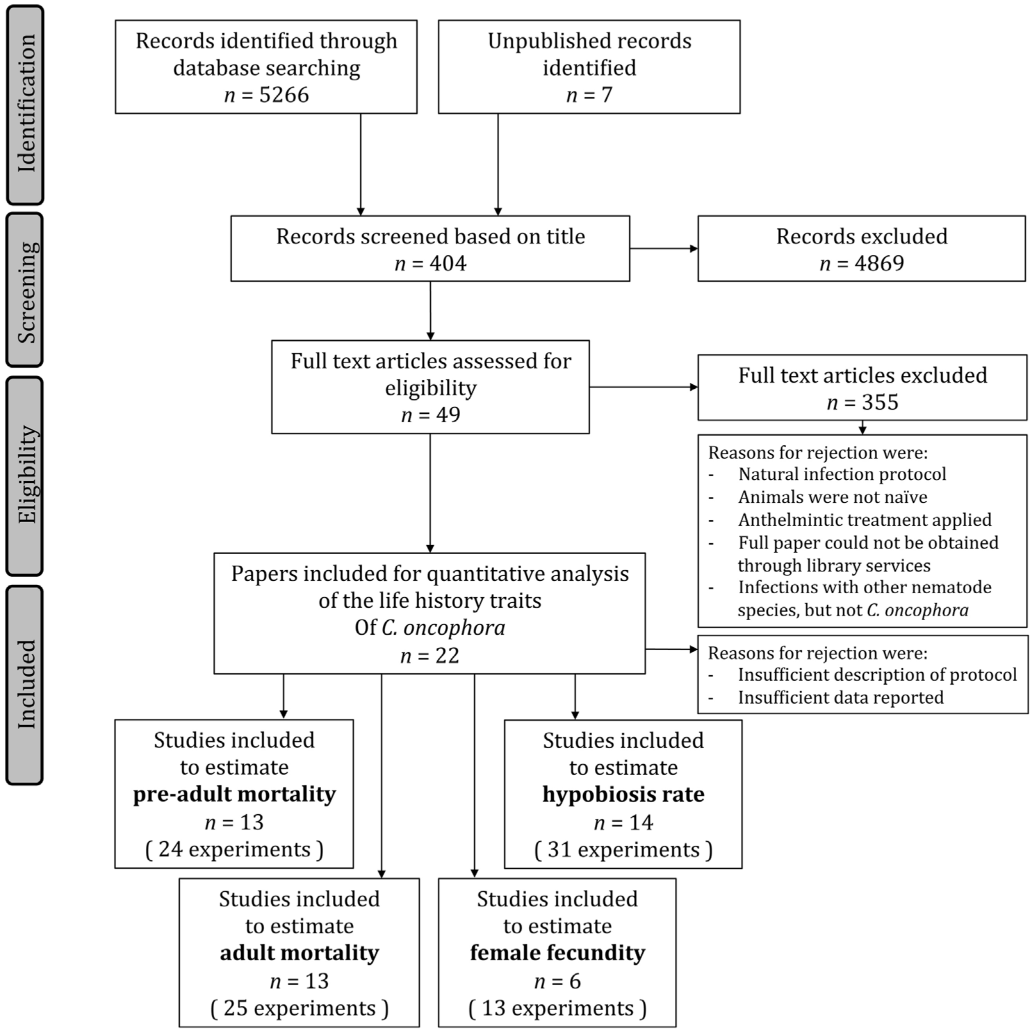

Fig. 1. Flowchart of the systematic review of key life history traits of the parasitic phase of *C. oncophora* and exclusion criteria for study selection to perform the meta-analysis. Adapted from PRISMA (Moher et al., 2009).

daily per capita death rate of pre-adult and adult stages, loosely interpreted as the proportion that die per day. The hypobiosis factor is defined as the proportion of ingested larvae that enters arrested development, and the female fecundity represents the number of eggs produced by a female worm each day. The search strategy and eligibility criteria used to perform the systematic review were the same as those described by Verschave et al. (2014). In short, studies in which naïve bovines were artificially infected with *C. oncophora* using a single or trickle infection protocol and that reported worm counts after necropsy with an associated measure of variance

Table 1
Equations used for the calculation of selected life history traits of the parasitic phase of *Cooperia oncophora* using meta-analysis, and the obtained estimates.

Parameter	Specific eligibility criteria concerning the duration of infection (days)	Estimate	Variance	Inverse variance weighted average	95% Confidence interval
Pre-adult mortality	21–40	$\frac{-\ln\left(\frac{AWB}{ID}\right)}{t}$	$\frac{var(AWB)}{t \times AWB}$	0.044	0.037–0.052
Adult mortality	>40	$\frac{-\ln\left(\frac{AWB}{ID}\right)}{t}$	$\frac{var(AWB)}{t \times AWB}$	0.039	0.031–0.048
Hypobiosis	>21	$\frac{eL4}{ID}$	$\frac{Var(eL4)}{ID^2}$	0.007	0.004–0.011
Female fecundity	>21	$\frac{(FEC \times DFP)}{(AWB \times F)}$	$\frac{DFP^2}{F^2} \times \frac{FEC^2}{AWB^2} \times \left(\frac{var(FEC)^2}{FEC^2} + \frac{var(AWB)^2}{AWB^2}\right)$	2744	1146–4342
Proportion of females (F)	>21	$\frac{FEM}{AWB}$	$\frac{FEM^2}{AWB^2} \times \left(\frac{var(FEM)}{FEM^2} + \frac{var(AWB)}{AWB^2}\right)$	0.534	0.494–0.573

Note: AWB = Adult worm burden; ID = Infection dose; t = duration of infection; eL4 = early L4 stages; FEC = faecal egg count at necropsy; DFP = Daily faeces production; F = Proportion of females; FEM = Number of adult female worms. Pre-adult mortality was estimated on duration of infection of 21–40 days to allow for establishment without being unduly affected by adult mortality (see Verschave et al., 2014 for a full explanation).