



Invited Review

Generalists at the interface: Nematode transmission between wild and domestic ungulates

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ABSTRACT

Many parasitic nematode species are generalists capable of infecting multiple host species. The complex life cycle of nematodes, involving partial development outside of the host, facilitates transmission of these parasites between host species even when there is no direct contact between hosts. Infective nematode larvae persist in the environment, and where grazing or water sources are shared ingestion of parasite larvae deposited by different host species is likely. In this paper we examine the extent to which nematode parasite species have been observed in sympatric wild and domestic ungulates. First, using existing host–parasite databases, we describe expected overlap of 412 nematode species between 76 wild and 8 domestic ungulate host species. Our results indicate that host-specific parasites make up less than half of the nematode parasites infecting any particular ungulate host species. For wild host species, between 14% (for common warthog) and 76% (for mouflon) of parasitic nematode species are shared with domestic species. For domestic host species, between 42% (for horse) and 77% (for llamas/alpacas) of parasitic nematode species are shared with wild species. We also present an index of liability to describe the risk of cross-boundary parasites to each host species. We then examine specific examples from the literature in which transmission of nematode parasites between domestic and wild ungulates is described. However, there are many limitations in the existing data due to geographical bias and certain host species being studied more frequently than others. Although we demonstrate that many species of parasitic nematode are found in both wild and domestic hosts, little work has been done to demonstrate whether transmission is occurring between species or whether similar strains circulate separately. Additional research on cross-species transmission, including the use of models and of genetic methods to define strains, will provide evidence to answer this question.

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1. Introduction

Parasites within the diverse class Nematoda infect a broad range of hosts including humans, domestic and wild animals, and plants (Blaxter et al., 1998). Nematodes are a ubiquitous part of an ecosystem and many are generalist parasites. In this paper we define a generalist parasite as a parasite species which has been found to

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survive and reproduce in more than one type of host in a given stage of its life cycle. The majority of parasitic nematodes have a multi-phase lifecycle, with a parasitic phase inside the host, and a free-living stage in the environment or intermediate hosts (Taylor et al., 2007). For most nematodes of ungulates, the definitive host is infected trophically, i.e. by ingesting infective larvae on pasture, though in some species larvae burrow through the skin or are transmitted by invertebrate intermediate hosts (Anderson, 2000). Trophic transmission of nematodes involves long-living infective stages and opportunistic exposure to hosts, and is therefore likely to provide an opportunity for infection of alternative host species (host switching).

In many parts of the world grazing land is shared between wild and domestic species, leading to the potential for transmission of parasitic nematodes between these groups. When studying the interactions between wildlife, livestock, and their parasites, it will be important to understand the historical context and patterns of contact and relatedness between the host species. If we are to make predictions of changes in host–parasite interactions due to climate or land use change at the interface between conservation areas and livestock-rearing areas, we must incorporate observations of existing host–parasite relationships with the possibility of host-switching. An extensive discussion of the theory of ecological fitting, whereby parasites possess the adaptations necessary to survive in a new host, and its implications for host-switching and the evolution of parasite generality is beyond the scope of this paper, but has been previously developed (Agosta and Klemens, 2008; Agosta et al., 2010; Hoberg and Brooks, 2008). A better understanding of the extent of and potential for cross-species transmission could influence management strategies for both domestic and wild ruminants in a variety of geographical contexts (Morgan et al., 2005).

Studies of disease transmission at the wildlife/livestock interface rarely discuss nematodes (Bengis et al., 2002; Gortázar et al., 2007; Kock, 2005; Wambwa, 2005). While other multi host diseases, such as foot and mouth disease and brucellosis, cause clear economic impacts on livestock producers, the role of nematodes is more subtle and nematodes on their own are not usually causes of high mortality. Nematodes have, however, been shown to strongly affect health, production, and population dynamics, even if these impacts have not been broadly quantified or generalized. It is difficult to estimate the total clinical impact of nematode infections because clinical signs are non-specific and dependent on the number of parasites in the host (Brooker, 2010). The economic cost of infection and of control of nematodes in the livestock industry is also difficult to estimate, in part because parasites can affect the productive value of animals in several different ways, including reductions in milk production, growth rate, fertility, and susceptibility to other diseases (Cobon and O'Sullivan, 1992; Perry and Randolph, 1999; Thumbi et al., 2013). For example, *Teledorsagia* (formerly known as *Ostertagia*, see Wilson et al., 2004) species contributed to mortality of Soay sheep during a malnutrition-related population crash, but the effect attributable to the parasites was not straightforward to calculate (Gulland, 1992). In wildlife, the seminal example of population-level impacts of nematodes is the regulation of population cycles in red grouse by *Trichostrongylus tenuis* (Hudson et al., 1998). Another gastrointestinal nematode parasite, *Ostertagia gruehneri*, was shown to have an effect on reindeer population density (Albon et al., 2002).

Historically, studies of nematode parasites in wild ruminants have been descriptive accounts rather than clinical, as knowledge of the morbidity and mortality that the parasites cause wild hosts is limited (Hoberg et al., 2001). In addition, few papers directly address transmission between wild and domestic hosts. For example, a long-running series of papers on parasites of domestic and wild animals in South Africa has documented the parasite fauna in different host species, but has not led to a published synthesis of the extent of

overlap between parasites of different host species (for example: Boomker et al., 1987; Horak et al., 2004; Van Wyk and Boomker, 2011). However, some regional reviews have been conducted addressing the extent of overlap between nematodes of domestic and wild ungulates, and these examples are discussed in Section 3.3. These accounts, while primarily descriptive, do include limited examples of a clinical or ecological perspective. In addition, while there has been much recent work on ecological theory related to host–parasite interactions, this is only beginning to be applied to the interface between wild and domestic ruminants (Hoberg et al., 2008).

In this paper we examine the extent to which nematode parasite species have been observed in sympatric wild and domestic ungulates globally. First, using existing host–parasite databases, we describe the extent to which parasite species overlap between wild and domestic ungulates is expected. We define a simple index of liability to compare host species by the extent to which their parasite fauna is specialized versus generalized, i.e. crossing the wild–domestic boundary. We then review the literature in which transmission of nematode parasites between domestic and wild ungulates is directly addressed, to demonstrate some of the limitations of current knowledge. The aim is to ascertain general patterns in recorded overlap of nematode fauna between wild and domestic ungulate species, in order to quantify the propensity of cross-transmission to occur in nature.

2. Methods

We reviewed known host–parasite associations in wild and domestic ungulates to determine the extent of overlap between nematode parasites in different host species. Nematodes of many wild ruminants have been described in the literature and these references compiled into the Global Mammal Parasite Database (GMPD) (Ezenwa et al., 2006). The GMPD includes references to parasite descriptions in wild artiodactyl and perissodactyl ungulates, including nematodes and other helminths, viruses, bacteria, and arthropods. A version of the database with citations from 1981 to 2002 is available online at www.mammalparasites.org. We used this online database as well as more recent records compiled by P.R. Stevens (unpublished data). Parasite names may be out of date in existing publications, so parasite species names are corrected during entry into GMPD according to current online databases (Nunn and Altizer, 2005). Various veterinary checklists for nematode parasites of domestic animals are available; we extracted these data from *Veterinary Parasitology* (Taylor et al., 2007). From this source, we were able to define the nematodes that parasitize domestic species: cattle, sheep, goats, pigs, horses, camels, and camelids (llamas and alpacas) (Taylor et al., 2007). A list of nematodes infecting donkeys and horses was also included (Matthee et al., 2004).

Records of parasitic nematodes in the GMPD which included a full binomial species name were included for the purposes of this analysis. Subspecies classifications for hosts and parasites were eliminated, and corrected binomial species classifications were used instead. Host–parasite associations which were recorded in the database but where prevalence was reported as zero were excluded.

Title, abstract, and/or full text of each reference was examined to find the geographic location of the study and whether multiple parasite species and/or multiple host species were included. References were categorized by geographical region (Polar, Asia and Pacific, Europe, Latin American and Caribbean, North America, West Asia, Africa) as defined by Global Environment Outlook 3 (GEO-3) of the United Nations Environment Program. A reference was considered to include multiple parasite species if it discussed multiple parasite species or diseases within the same animal. Papers that assessed, discussed, or inferred transmission of nematodes between wildlife and livestock were identified for further review.

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