

Nematode co-infection dynamics: exploring variation in wild sheep

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Co-infections with multiple species of gastrointestinal nematodes (GIN) cause significant impacts on human health and development, wild animal survival and fitness, and livestock welfare and productivity. The prevalence and intensity of these co-infections are subject to complex dynamics, and the management of them is further complicated by anthelmintic resistance and climate-linked temporo-spatial changes in the different species' epidemiologies. Wild animal systems are well suited to studying these dynamics in the absence of human interventions and, in addition to advancing our fundamental understanding of disease ecology, may inform alternative management strategies with reduced reliance on anthelmintics.

The wild Soay sheep of St Kilda provide an ideal such system, given their unmanaged nature and transferable tools developed in domestic sheep. Here we apply ITS-2 sequence-based nematode speciation (The Nemabiome) to approximately 2000 faecal samples collected non-invasively up to four times annually from over 500 Soay sheep over a four-year period. These species proportions are then corrected for faecal egg count and analysed using modern mixed-modeling approaches, incorporating the wealth of host phenotypic data for which this study system is renowned.

Our analyses of these data reveal seasonal epidemiological patterns in *Nematodirus battus* and *Teladorsagia circumcincta* that are consistent with those observed in managed domestic sheep and are well explained by temporal variation in egg shedding and the free-living ecologies of these species. However, contrary to expectations derived from experience in domestic sheep, *Trichostrongylus vitrinus* is found at consistent levels throughout lambs' first year of life, whilst levels of *Trichostrongylus axei* rise into the early spring of the second year of the sheep's life. These differences are similar to early reports of seasonal infections in domestic sheep prior to modern anthelmintics, but are not easily explained by the ecologies of the free-living larval stages alone, raising important questions about within-host dynamics. Our work also sheds important insight into the epidemiology of *Bunostomum trigonocephalum* a poorly studied nematode parasite of sheep that was considered a significant parasite in the UK prior to widespread anthelmintic use and continues to cause impacts in other global settings. Our results then show further variation in nematode co-infections between males and females of different ages, leading on to planned investigations into whether co-infection patterns are repeatable or heritable under natural conditions.