

Research Paper

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# Epidemiological approach to nematode polyparasitism occurring in a sympatric wild ruminant multi-host scenario

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## Abstract

The epidemiology behind multi-host/multi-parasite systems is particularly interesting to investigate for a better understanding of the complex dynamics naturally occurring in wildlife populations. We aimed to approach the naturally occurring polyparasitism of gastrointestinal nematodes in a sympatric wild ruminant scenario present in south-east Spain. To this end, the gastrointestinal tract of 252 wild ruminants of four different species (red deer, *Cervus elaphus*; mouflon, *Ovis aries musimon*; Iberian ibex, *Capra pyrenaica* and fallow deer, *Dama dama*) were studied in Cazorla, Segura y Las Villas Natural Park (Andalusia, Spain). Of the analysed animals, 81.52% were positive for parasite infection and a total of 29 nematode species were identified. Out of these, 25 species were detected in at least two host species and 11 parasitized all ruminant species surveyed. The multi-host interaction between these nematodes and the four host species is discussed under the perspective of host family-based differences.

## Introduction

Gastrointestinal nematodes are common parasites of herbivores. Usually, a single host is infected by several nematode species distributed along the abomasum, small intestine and large intestine. Additionally, it is quite frequent to find different host species sharing the same parasite species. This is due to nematode egg dispersal through faeces and, consequently, to the presence of infective larvae in areas where several susceptible host species share the same trophic resources. Thus, parasite transmission and infection rates involve highly stochastic dynamics (Cornell, 2005) including intrinsic and extrinsic factors such as host immune status, host behaviour or climate conditions (Agosta & Klemens, 2008; Hoberg & Brooks, 2008; Agosta *et al.*, 2010). These interactions have increased interest on how parasite exchanges between host species may affect closely related hosts (Morgan *et al.*, 2004; Obanda *et al.*, 2019), a process that becomes most notorious in natural ecosystems where different host species share the same habitat.

The multi-host parasite paradigm has proven itself particularly useful to study the role of pathogens influencing wildlife population dynamics (Smith *et al.*, 2006; Delogu *et al.*, 2013; Sinclair *et al.*, 2016; Leivesley *et al.*, 2019). Examples have been documented in literature for closely related ungulates as showcased by a recent study dealing with sarcoptic mange by Iacopelli *et al.* (2020); this study describes a spatio-temporal pattern of sarcoptic mange infection data in two wild ruminants in south-east Spain, showing that the disease is directly responsible for the decline of Iberian Ibex (*Capra pyrenaica*) populations. Although gastrointestinal nematode infections usually cause no clinical signs in wild ruminants (Gunn & Irvine, 2003), nematode burden has shown to exert a negative impact on wild ungulate population dynamics (Gulland, 1992; Albon *et al.*, 2002). However, the gastrointestinal multi-host/multi-parasite system parasite richness occurring in sympatric wild ruminants in south-east Spain still remains to be studied (Parker *et al.*, 2003).

Wild ruminants have been shown to be highly exposed to pathogens due to the variety of their grazing resources, often shared with domestic ruminants as well (Ocaido *et al.*, 2004). Sierras de Cazorla, Segura y Las Villas Natural Park (SCSV) is the largest protected area in Spain, harbouring a wide array of habitats and trophic resources to host four different wild ungulates: mouflon (*Ovis aries musimon*), red deer (*Cervus elaphus*), fallow deer (*Dama dama*) and Iberian ibex. Grazing by livestock (mainly small ruminants) is allowed in

**Table 1.** Total animal census during the sampling period.

Year	Iberian ibex	Mouflon	Red deer	Fallow deer	Total
2000	1778	1396	1633	1530	6337
2001	1908	1368	1733	1396	6405
2002	ND	ND	ND	ND	ND
2003	1965	1214	1903	1310	6392
2004	2107	1226	1881	1405	6619

ND, not determined.

peripheral areas of SCSV, with clearly defined park boundaries within which the presence of any livestock species is forbidden (BOJA, 2017; PORN, 2017). Given this background, we aim to compare patterns of parasite abundance and the degree of parasite sharing within the naturally occurring multi-host parasitism affecting these four wild ungulates. The SCSV is a paradigmatic area to study parasite transmission among ruminants in a multi-host/multi-parasite system. In view of the prevalence and impact that nematodes might have on wild ruminants, a better understanding of their dynamics could shed further light on the epidemiology of polyparasitism and, consequently, favour the management and conservation of their populations.

## Material and methods

### Area of study and collection of the samples

The Sierras de Cazorla, Segura y Las Villas Natural Park (SCSV) is the second largest protected area in Europe. It is located on the eastern side of the Baetic Mountains (Andalusia, Spain), spanning an area of 2140 km<sup>2</sup> (Fandos, 1991). The area has a Mediterranean mountain climate with mild winters and hot summers. The average annual precipitation is less than 448 mm and the average annual temperature of 15°C.

We collected 252 digestive tracts from February to April throughout the years 2003 to 2005 from a set of wild ruminants including two cervid species, fallow deer ( $n = 109$ ) and red deer ( $n = 64$ ); and two bovids, mouflon ( $n = 59$ ) and Iberian ibex ( $n = 20$ ). Samples originated from free-ranging animals hunted at SCSV an integral part of wildlife population control, the estimated annual census for each ruminant species in the park is listed in table 1. Mouflon and fallow deer were introduced in the 1950s of the last century for hunting purposes, while Iberian ibex and red deer are native species in the study area (De Leyva, 2002; Herrera, 2008; Masseti & Mertzaniidou, 2008; Cassinello & Salvador Milla, 2017).

All animal manipulations were performed according to the Animal Care Committee guidelines and the Bioethical Committee of Murcia University (Murcia, Spain), the local Committees for animal research (REGA ES300305440012), and in accordance to the current European Animal Welfare Legislation (ART13TFEU).

### Collection, storage and identification of parasites

Field necropsy was performed immediately after animals were shot by park rangers, and the whole digestive tract was removed. In order to record the exact location of the nematodes along the tract, each section was clamped, double ligated and preserved in identified plastic bags until further laboratory processing. Then,

gastrointestinal nematodes were collected by separate processing of abomasum, small and large intestines. Following a longitudinal cut, mucosae of each digestive section were examined by scraping. Digestive tract content was washed and sieved through a series of mesh screens (mesh pore sizes: 1 cm, 0.6 mm and 0.3 mm). The resulting sediment was preserved in 10% formalin samples.

Samples from abomasum and small intestine were diluted with water up to 2 l, and thoroughly mixed. One aliquot, representing 10% of the volume was examined in small portions under a stereoscopic microscope to collect the nematodes. When there were not sufficient nematodes for identification purposes (up to 100 individuals), one or two more aliquots (up to a total of 30% of the volume) were analysed. Male and all female nematodes were collected but only male specimens were identified. The number of male nematodes was expanded to the whole sample volume in order to calculate the abundance of each parasite species. In the specific case of the large intestine, all nematodes present were counted.

Morphometric characteristics were used to categorize the adult male parasites by species following Durette-Desset (1989) for the sub-family Ostertagiinae, and Skrjabin *et al.* (1961) and Yamaguti (1961) for the Strongylida suborder. All nematode specimens were analysed as described by Ortiz *et al.* (2001).

### Epidemiological parameters and statistical analysis

Prevalence, intensity and abundance of infection for each parasitic species were defined according to Margolis *et al.* (1982) and Bush *et al.* (1997). Briefly, prevalence is defined as the number of hosts infected with a particular parasite species (or taxonomic group) within the number of hosts examined, expressed as a percentage; intensity is defined as the number of individuals of a particular parasite species in a single infected host, expressed as the number of specimens per infected animal; and abundance is defined as the number of individuals of a particular parasite species per host examined. At a population level, the intensity refers to the mean number of parasites within infected members of that host population (hence excluding uninfected hosts). In contrast, abundance refers to the mean number of parasites within the entire studied host community. Fisher's exact test was used to analyse the prevalence at different host population levels. A model-based analysis of multivariate abundance data was used to evaluate frequency distribution of the abundance for the parasites shared by the four host species. Multivariate analysis of parasite abundance was carried out using the mvabund package (Wang *et al.*, 2012). Subsequently, Kruskal-Wallis analysis was performed to statistically test the outcome. Analyses were carried out using R software (RStudio Team, 2015).

## Results

### General descriptive patterns of the gastrointestinal nematodes

Twenty-nine nematode species were found and 81.52% of the analysed ruminants were parasitized with nematodes at least in one gastrointestinal section. *Spiculoptera* *asymmetrica* (55.9%), *Oesophagostomum venulosum* (58.7%) and *Spiculoptera quadripiculata* (45.3%) were the most prevalent species overall. All identified nematode species, as well as their respective prevalence, abundance and intensity are listed in table 2.

Prevalence values differed among the host species. Fallow deer presented the highest nematode prevalence ( $n = 109$ ; 91.5%),

**Table 2.** List of identified nematode species and their prevalence, abundance and intensity per host.

	Total		Iberian Ibex <i>Capra pyrenaica</i>			Mouflon <i>Ovis aries musimon</i>			Fallow deer <i>Dama dama</i>			Red deer <i>Cervus elaphus</i>		
	P (%)	I.R.	P (%)	A	I.R.	P (%)	A	I.R.	P (%)	A	I.R.	P (%)	A	I.R.
<b>TOTAL</b>	81.5	1–2034	83.3	319.9	1–1076	85.5	630.3	1–2873	91.5%	260.5	1–338	61.4	140.86	1–1475
<b>Abomasum</b>	79.0	1–2873	100.0	283.9	2–1076	100.0	436.9	1–2873	88.9	150.8	2–608	97.9	260.4	1–1475
<i>Haemonchus contortus</i>	5.3	2–50	14.3	3.1	2–41	28.9	5.1	3–50	0.0	0.0	0	0.0	0.0	0
<i>Teladorsagia circumcincta</i>	24.3	1–1957	92.9	163.2	8–406	93.3	348.6	5–1957	8.9	4.4	1–145	0.0	0.0	0
<i>Teladorsagia trifurcata</i>	20.2	2–473	71.4	18.7	3–93	73.3	47.0	3–473	4.4	0.2	2–5	4.3	1.4	7–64
<i>Teladorsagia davtiani</i>	1.6	2–30	0.0	0.0	0	8.9	1.3	2–30	0.0	0	0	0.0	0.0	0
<i>Ostertagia ostertagi</i>	0.6	3–30	0.0	0.0	0	0.0	0	0	2.2	0.3	3–30	0.0	0.0	0
<i>Ostertagia leptospicularis</i>	33.2	1–156	14.3	1.1	5–11	11.1	0.9	2	60.0	11.8	3–73	52.7	11.6	1–156
<i>Ostertagia kolchida</i>	12.1	2–47	0.0	0.0	0	2.2	0.5	4–15	20.0	1.3	2–12	23.7	3.3	2–47
<i>Spiculopteragia asymmetrica</i>	55.9	1–1355	42.9	5.6	2–62	17.8	1.0	21	82.6	100.6	1–413	93.5	189.9	1–1355
<i>Spiculopteragia quadrispiculata</i>	45.3	1–178	21.4	1.1	2–10	2.2	23.5	1–22	75.6	19.5	1–109	79.6	40.2	3–178
<i>Trichostrongylus axei</i>	22.7	2–807	35.7	65.3	4–807	60.0	0.7	2–414	20.0	10.1	2–274	16.1	8.7	2–212
<i>Marshallagia marshalli</i>	4.5	1–19	35.7	3.2	1–19	6.8	0.5	3–17	2.2	0.4	17	0.0	0.0	0
<i>Ostertagia occidentalis</i>	0.8	10	7.1	0.7	10	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0
<i>Marshallagia dentispicularis</i>	2.8	3 105	28.6	17.8	18–105	0.1	0.0	4	2.2	0.1	3	0.0	0.0	0
<b>Small intestine</b>	50.6	1–2034	100.0	94.1	3–295	83.9	239.1	1–2034	34.6	4.6	1–158	42.9	7.6	1–129
<i>Nematodirus filicollis</i>	3.2	2–44	11.8	0.9	4–11	9.1	1.8	2–44	1.9	0.1	6	0.0	0.0	0
<i>Nematodirus abnormalis</i>	10.5	3–256	82.4	49.6	3–256	20.0	6.3	4–187	1.9	0.3	18	1.0	0.1	4
<i>Nematodirus spathiger</i>	12.1	2–257	47.1	9.4	3–74	38.2	16.4	2–257	1.9	2.3	117	0.0	0.0	0
<i>Trichostrongylus vitrinus</i>	23.9	1–725	70.6	11.2	1–54	65.5	62.0	2–725	1.9	0.1	6	10.4	3.1	1–93
<i>Trichostrongylus colubriformis</i>	2.4	2–6	0.0	0.0	0	7.3	0.3	3–6	0.0	0.0	0	2.1	0.1	2–4
<i>Trichostrongylus capricola</i>	23.1	2–1493	70.6	23.0	2–114	65.5	143.5	4–1493	1.9	0.3	18	8.3	2.2	3–68
<i>Cooperia oncophora</i>	1.6	5–21	0.0	0.0	0	0.0	0.0	0	5.8	0.4	5–12	1.0	0.2	21
<i>Cooperia pectinata</i>	0.4	10	0.0	0.0	0	0.0	0.0	0	0.0	0	0	1.0	0.1	10
<i>Cooperia surnabada</i>	0.4	3	0.0	0.0	0	0.0	0.0	0	0.0	0	0	1.0	0.0	3
<b>Large intestine</b>	66.8	1–338	88.2	12.9	1–105	79.6	25.4	1–195	92.2	31.1	1–338	51.1	3.2	1–57
<i>Oesophagostomum venulosum</i>	58.7	1–338	70.6	4.5	1–45	59.3	9.1	1–159	87.5	30.5	1–338	47.9	2.6	1–52
<i>Chabertia ovina</i>	22.7	1–128	52.9	1.7	1–9	66.7	15.0	1–128	3.1	0.0	1–2	9.6	0.1	1–3
<i>Trichuris globulosa</i>	9.7	1–12	0.0	0.0	0	25.9	0.9	1–12	3.1	0.0	1–2	8.5	0.2	1–5
<i>Trichuris ovis</i>	6.1	1–6	5.9	0.1	2	6.8	0.1	1–2	9.4	0.1	1	4.3	0.1	1–6

(Continued)

Table 2. (Continued.)

	Total		Iberian ibex <i>Capra pyrenaica</i>		Mouflon <i>Ovis aries musimon</i>		Fallow deer <i>Dama dama</i>		Red deer <i>Cervus elaphus</i>		
	P (%)	I.R.	P (%)	A	I.R.	P (%)	A	I.R.	P (%)	A	I.R.
<i>Trichuris discolor</i>	2.4	1-3	0.0	0.0	0	1.9	0.0	1	3.1	0.0	1-2
<i>Trichuris skrjabini</i>	4.0	1-5	0.0	0.0	0	13.0	0.1	1-5	1.6	0.0	1
<i>Skrjabinema ovis</i>	2.0	1-95	29.4	6.6	1-95	0.0	0.0	0	0.0	0.0	0

P: Prevalence; A: Abundance; I.R.: Intensity Range.

followed by the wild bovids (mouflon  $n = 59$ , 85.5%; Iberian ibex  $n = 20$ , 83.3%) and the red deer ( $n = 64$ , 61.4%). For more details see supplementary material (S1).

Richness in nematode species was different between host species: mouflon and fallow deer were found to host up to 12 different species, followed by Iberian ibex and red deer, where up to ten and seven different nematode species were isolated, respectively (fig. 1 and table 2). Our results showed a significantly positive correlation between nematode species richness and intensity (fig. 2c, d). This correlation was significant for all analysed hosts, with the mouflon and the red deer presenting the highest correlation (see supplementary material, S2).

### Multi-host nematode distribution

Eleven nematode species were commonly found parasitizing all host species: *Teladorsagia trifurcata*, *Ostertagia leptospicularis*, *S. asymmetrica*, *S. quadrispiculata* and *Trichostrongylus axei*, *Nematodirus abnormalis*, *Trichostrongylus vitrinus*, *Trichostrongylus capricola*, *O. venulosum*, *Chabertia ovina* and *Trichuris ovis*.

Except for *T. ovis*, prevalence for the above mentioned species differed significantly between cervids and bovids, as represented in fig. 3. Mean abundance differed significantly between host species as shown in fig. 4a. Additionally, the abundance of these 11 species showed significant differences among hosts (fig. 4b). In particular, we identified different parasite communities on different host species (likelihood ratio test – LRT = 613.6;  $P < 0.001$ ). The differences among host species are maintained even at the parasite species level (adjusted for multiple testing), with the exception of *T. ovis* (LRT = 0.431;  $P > 0.05$ ) and *T. axei* (LRT = 0.498;  $P > 0.05$ ). The differences at the parasite community level (adjusted for multiple testing) were significant even between bovids and cervids (LRT = 472.5;  $P < 0.001$ ) (fig. 4b). In this case the univariate analysis adjusted for multiple testing confirmed the significant differences at the single species level for all parasite species with the exception of *T. axei* (LRT = 1.886;  $P > 0.05$ ), *O. venulosum* (LRT = 2.685;  $P > 0.05$ ) and *T. ovis* (LRT = 0.078;  $P > 0.05$ ) (supplementary fig. S1).

### Single-host nematode distribution

The Iberian ibex was the only ungulate to be infected by *Marshallagia occidentalis* and *Skrjabinema ovis* with 7.1% and 29.4% prevalence, respectively. Likewise, 2.2% of the red deer were also infected with *Ostertagia ostertagi* in the abomasum, with an average intensity of 13 nematodes per host (table 2). Similarly, *Cooperia pectinata* and *C. surnabada* were only reported in the small intestine of fallow deer, showing 1.0% prevalence and intensities of 21 and ten nematodes per host, respectively. Finally, mouflon was the only host species in which *Teladorsagia davtianii* was isolated from the abomasum, with a prevalence of 8.9% and an intensity range of 2–30 nematodes (table 2).

### Discussion

Our study highlights the occurrence of a very rich and diverse parasite community shared among wild ungulates in SCSV. It represents a clear example of a multi-parasite/multi-host scenario in which the vast majority of nematodes are shared between at least two sympatric host species and only a few parasites are exclusive to a single host species. The structure of the parasite community was significantly host influenced, with the highest parasite

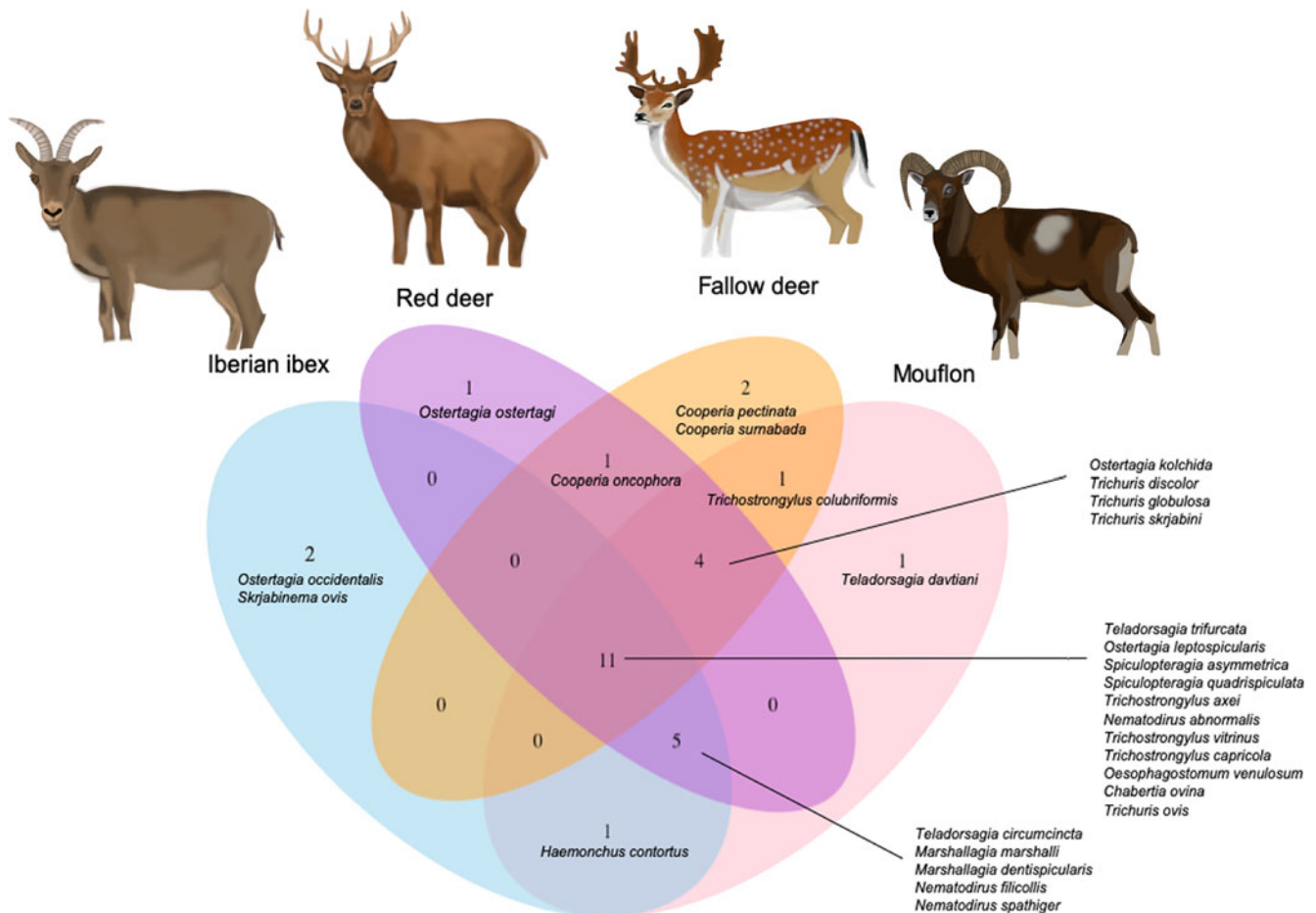


Fig. 1. Venn diagram representing the nematode species found in each species of wild ruminant host.

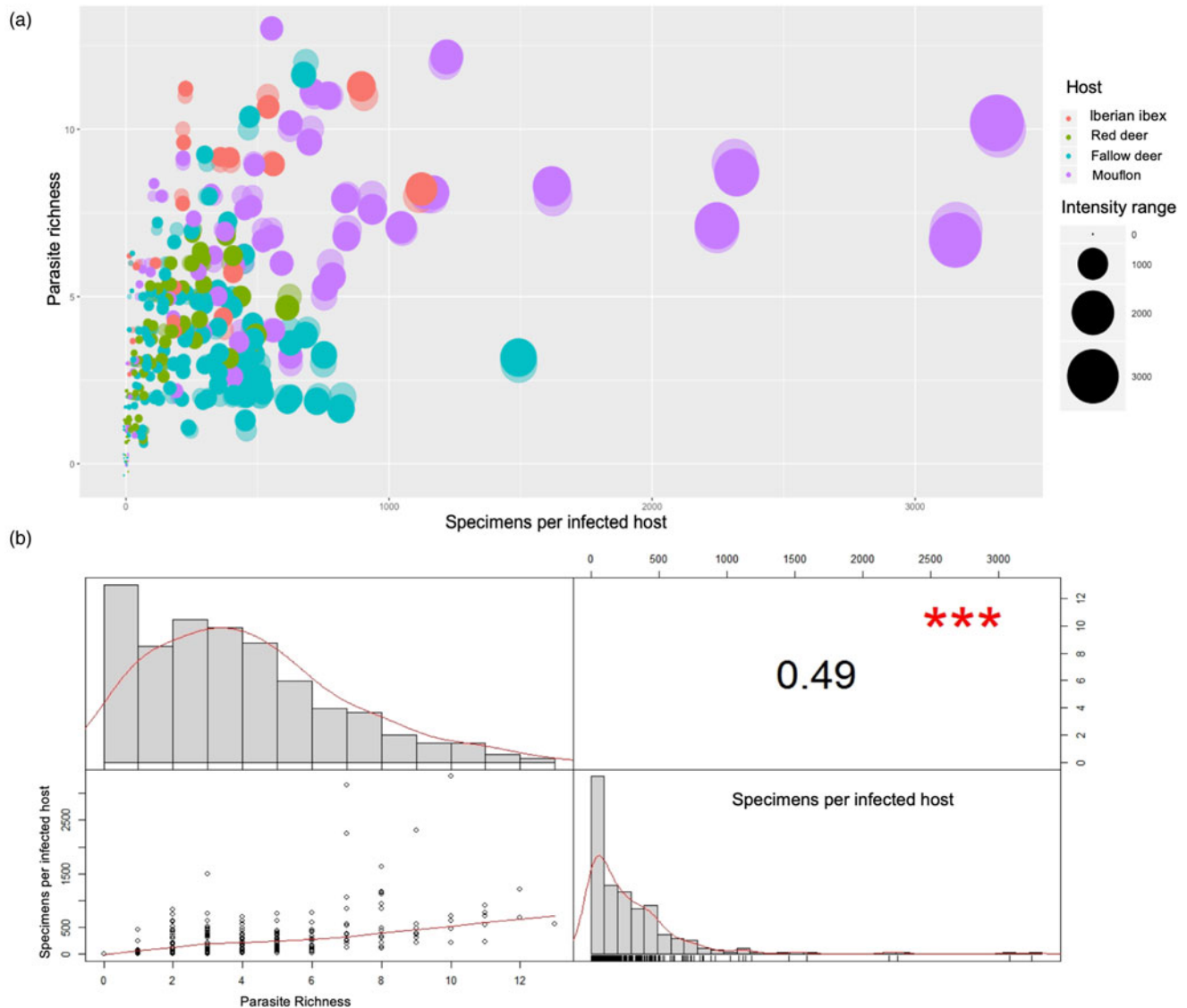
prevalence and richness consistently appearing in mouflon and fallow deer hosts. These results were confirmed through an innovative model-based approach to the analysis of multivariate abundance data (Yee, 2010; Ives & Helmus, 2011; Ovaskainen & Soininen, 2011), that provides more accurate results than traditional distance-based methods (Warwick *et al.*, 1990).

Wild animals are more likely to host a larger parasite richness in comparison with livestock because of increased exposure to infective stages in natural areas (Bordes *et al.*, 2009; Walker & Morgan, 2014). Macroparasites are important components of ecological communities (Pedersen & Fenton, 2007), with single-host polyparasitism being a common state for many wild animals (Cox, 2001; Polley & Thompson, 2015). Ecological interactions and their implications in polyparasitism and multi-host co-infection must be understood to better explain parasite patterns of richness and diversity (Craig *et al.*, 2008; Morand, 2015). From this integrative perspective, SCSV offers a perfect scenario for the study of a natural multi-host/multi-parasite system, since it is a large natural area with four sympatric wild ruminant species that interact with domestic livestock.

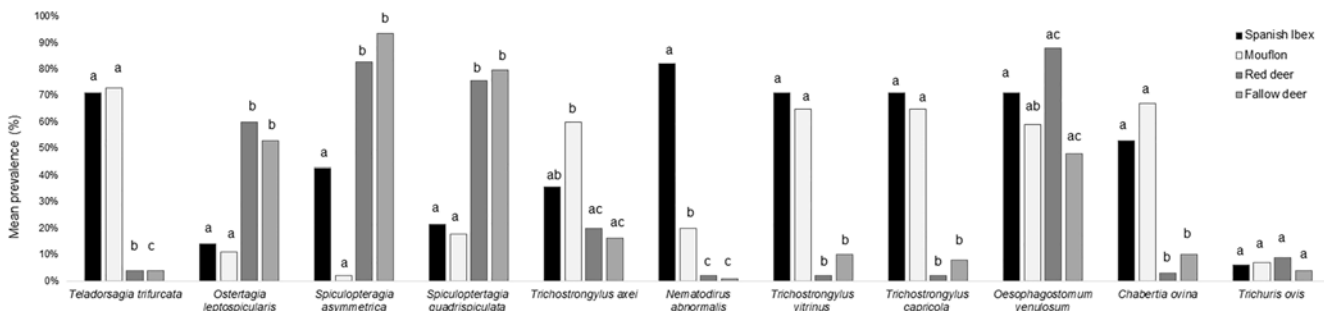
We have recorded up to twenty-nine nematode species belonging to the superfamilies Strongyloidea and Trichostrongyloidea, the latter being the most dominant in our study because of its higher species diversity (Hoberg & Lichtenfels, 1994). Potentially pathogenic genera, such as *Ostertagia* and *Haemonchus*, as well as individual species such as *C. pectinata*, *O. venulosum*, *C. ovina* and

*T. ovis* were found in our study. Previous studies have reported that these nematodes can have a negative impact on both domestic and wild ruminants (Herlich, 1965; Jackson *et al.*, 1988; Parkins & Holmes, 1989; Lavín *et al.*, 1997). The repercussion of gastrointestinal nematodes on wildlife is also well known, and previous studies have already shown that gastrointestinal nematodes reduce food intake in parasitized cervids and/or cause severe lesions that can lead to reduced weight gain (Gulland, 1992; Arneberg *et al.*, 1996; Lavín *et al.*, 1997; Coltman *et al.*, 1999; Albon *et al.*, 2002; Fanelli *et al.*, 2020).

Interestingly, parasite richness varied greatly among hosts, ranging from one to up to twelve different nematode species in a single host. The parasite richness found in the mouflon population was particularly high. This wild ruminant was introduced in Spain for hunting purposes in 1953 (Cassinello & Salvador Milla, 2017). When allochthonous species are introduced in a new ecosystem, their successful reproduction, colonization of new habitat and eventual occupation of existing ecologic niches, can result in a threat to local biodiversity through the displacement of native species (Hulme *et al.*, 2009; Kelly *et al.*, 2009). The mouflon has adapted extremely well to its new habitat in the Iberian Peninsula (Cassinello & Salvador Milla, 2017) and, as demonstrated in our study, to the parasite fauna of its sympatric ruminant community. The mouflon may act as an efficient spreader of parasites, as it shares the same pastures with other wild bovids such as the Iberian Ibex in winter and in spring



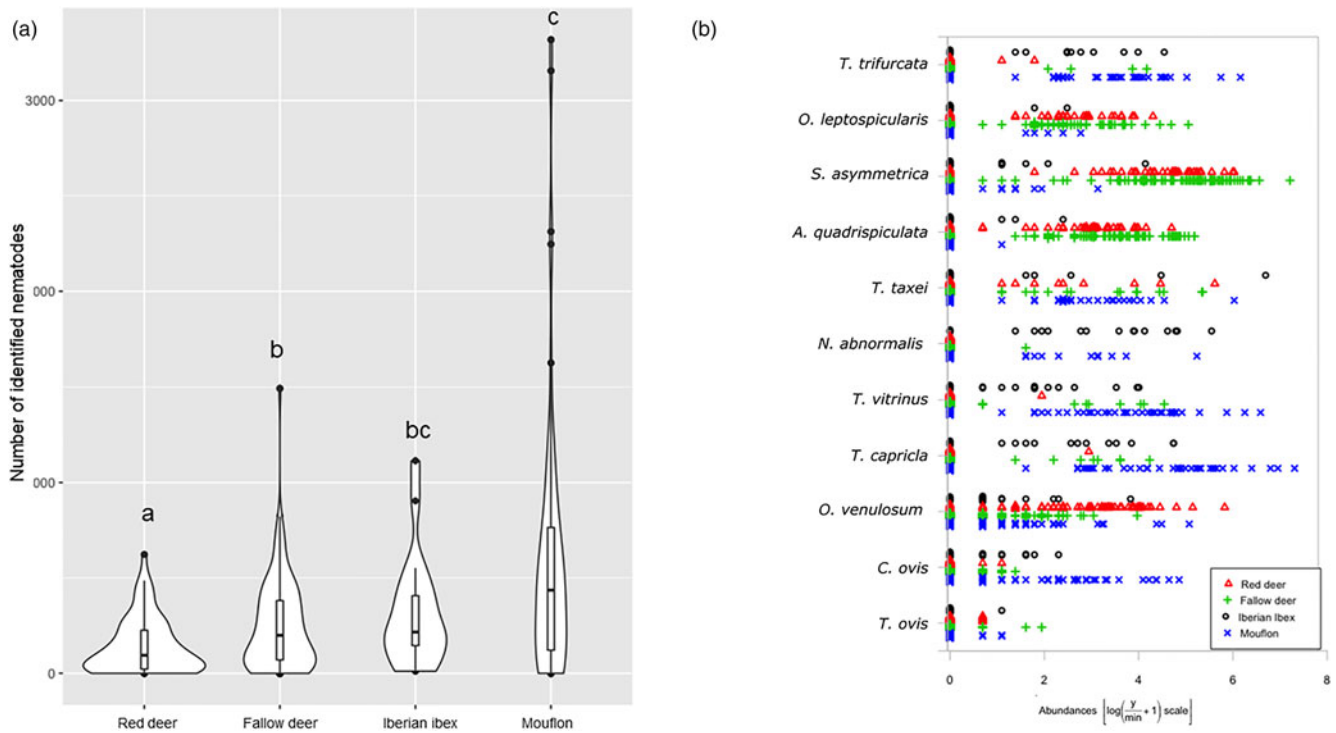
**Fig. 2.** Richness and intensity was evidenced in this study as shown by the bubble plot (a) and significantly represented in the correlogram (b).  $P$  values lower than 0.05 were considered statistically significant: \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.0001$ .



**Fig. 3.** The mean nematode prevalence of the eleven commonly found species showed significant differences between hosts. Different letters indicate significant effect.

(Martínez & Fandos, 1989), and in summer with cervids, such as red deer (Miranda *et al.*, 2012). Moreover, this allochthonous species shares the majority of its gastrointestinal parasites with domestic sheep (Pisanu *et al.*, 1996; Balicka-Ramisz *et al.*,

2017). In fact, cross-infection has been described by Bartczak & Okulewicz (2014), whose work evidenced that the mouflon may play a significant epidemiological role in the exchange of parasites between cervids and domestic ruminants (sheep and goats).



**Fig. 4.** Abundance of total identified nematodes (a) and the 11 commonly found parasite species (b) described in all studied wild ruminants (b). Different letters indicate significant effect.

Under this perspective, the mouflon might act as an epidemiological link of nematode transmission between wild ruminants and small ruminant farms located in the peripheral area of the SCSV, where livestock is allowed to graze (Walker & Morgan, 2014).

Furthermore, parasite richness was linked to higher parasite intensity for all wild ruminant species. This may be due to a combination of several factors including high host population density (Ezenwa, 2004), the direct life cycle of some macroparasites that may facilitate transmission rate (Arneberg, 2001), and environmental changes that affect host/parasite-mediated speciation (Brunner & Eizaguirre, 2016). The abundance and intensity patterns of some parasites, such as *T. circumcincta*, *T. trifurcata*, *T. vitrinus* and *T. capricola*, among others, have been directly related to rainfall, which tend to increase in intensity during spring (Valcárcel & Romero, 1999). Nonetheless, further studies should be carried out to understand the influence of external and/or internal factors on the gastrointestinal nematode intensity and richness in its wild ruminant community (Ortiz *et al.*, 2001).

Finally, differences in the abundance pattern of some nematodes were also observed. The presence of specific patterns was highlighted by the multivariate analysis of abundance, which demonstrated significant differences among the 11 nematode species shared by all host species. Clear patterns were observed at both the host species (fallow deer, Iberian ibex, mouflon and red deer) and the host group levels (bovids vs. cervids). These findings highlight the ability of parasites to adapt to the community of hosts and shape their ecological distribution according to the most suitable host species available (Winter *et al.*, 2018).

The clearest example under this perspective is represented by the nematode species in the abomasum, which were found in all host species but with significantly higher intensity in cervids than in bovids. This dichotomous pattern has already been

reported by Zaffaroni *et al.* (2000). In particular, *S. asymmetrica* is usually found parasitizing the gastrointestinal tract of cervids (Drózdź, 1966; Santín-Durán *et al.*, 2004) and is rare in sylvatic and domestic bovids (Suarez & Cabaret, 1991). A positive association has already been described between strongyle co-infection prevalence and level of habitat overlap across taxa. This is because sharing of nematodes is more likely in closely related hosts because of their similar ecology, physiology and behaviour (Ezenwa, 2003; Gruijter *et al.*, 2004; Ocaido *et al.*, 2004; Archie & Ezenwa, 2011).

## Conclusion

The results of our study may represent a baseline to be considered for the planning and implementation of wild ruminant management projects. We consider that evaluating nematode richness, prevalence and intensity is helpful to better understand the health situation of free-ranging ruminants, in particular when multiple hosts share the same area in high population densities. An additional but non-negligible benefit in understanding and eventually reducing the impact of diseases linked with overabundance is represented by the fact that they can affect not only fitness and trophy quality, but also human and livestock health, as well as the success of conservation measures for endangered species.

**Supplementary material.** To view supplementary material for this article, please visit <https://doi.org/10.1017/S0022149X21000183>

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