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“Till death do us apart”: The common destiny of brown hare and its parasite community

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ABSTRACT

Although parasites may threaten individual hosts' survival and reproduction, their role as an essential part of ecosystem functioning and biodiversity has been recognized. In Northern Italy, the hare population has evidently declined since 2008.

This paper aims to assess the relationship between host demographic trends and helminth parasite community diversity in a two-year survey in Northern Italy to evaluate the impact of parasites on hosts and confirm the hypothesis that endangered host populations are poor in parasites.

In 2013 and 2015 the viscera of 54 and 61 hares legally hunted in agro-ecosystems of the Po Plain were collected. This area is characterized by heavy anthropic pressure: more than 60% of the landscape is represented by agricultural or urbanized territories.

No intestinal cestodes were detected. *Trichuris* sp. and *Micipsella numidica* were collected in 2015 only; *Trichostrongylus retortaeformis*, *Taenia pisiformis* cysticercosis and bronchopulmonary lesions caused by small strongyles were observed in both years. The richness and evenness appeared increased in the second year of the survey, although lower than those obtained by literature data from similar populations examined in the last two decades of 1900.

The dominant helminth, *T. retortaeformis*, was more abundant in individuals with higher weight, while pathological findings were mostly unrelated to this nematode infection; this is consistent with a reduced action, even no harm, of the parasites on the individual host or population level.

Our results suggest that the conservation of hosts, environment, and parasites cannot be achieved separately and that parasites and wildlife hosts' destinies are intimately linked, confirming the complexity of ecosystems and the need to contemplate parasite biodiversity in conservation strategies.

1. Introduction

In the last 50 years, a reduction of the European hare population (*Lepus europaeus*) has been recorded in most European Countries (Edwards et al., 2000; Schmidt et al., 2004; Smith et al., 2005).

The slope of hare population decline has gotten worse since 2008 in Northern Italy, particularly in the Emilia Romagna region (Zanin, 2017), wherein in 2013 and 2015, a survey about helminth infections in European hares was undertaken. The first results of this survey published by Stancampiano et al. (2019), suggested both a possible role of *Taenia pisiformis* cysticercosis on host population health and a tendency toward host-parasite equilibrium over two years. In the present paper, we investigated the whole helminth community of the same declining population of European hares.

Although parasites may threaten individual hosts' survival and reproduction, their role as an essential part of ecosystem functioning and biodiversity has been definitely recognized (Lafferty, 2014; Carlson et al., 2020). Some authors hypothesized that parasite community biodiversity is higher in healthy host populations and ecosystems (Marcogliese, 2005; Hudson et al., 2006; Johnson et al., 2013). Certainly, environmental pollution can be toxic for free-living parasite stages and anthropization can determine the loss and fragmentation of habitat for both definitive and intermediate hosts (Lafferty, 2014; Marcogliese, 2023). In addition, any pressure decreasing host population density is expected to influence the richness of parasite communities negatively (Morand, 2000; Deredec and Courchamp, 2003); in the case of European hare living in the study area, the population management could have acted as an additional detrimental factor thanks to

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the strong exploitation implemented by hunters and to the following capture from protected areas and release in hunting territories usually carried out after the hunting seasons (Zanin, 2017, 2022).

Ten years ago, Gómez and Nichols (2013) suggested the inclusion of parasite biodiversity in conservation strategies. This paper, evaluating parasite community and parasite distribution in relation to host parameters, aimed to assess the relationship between host demographic trends and helminth parasite community diversity in a two-year survey in Northern Italy to evaluate the impact of parasites on hosts and confirm the hypothesis that endangered host populations are poor in parasites. Hopefully, this will add empirical data for parasites to be fully considered part of biodiversity.

2. Material and methods

In 2013 and 2015 the viscera of 54 and 61 hares legally hunted in agroecosystems of the Po Plain were collected, as detailed in Stancampiano et al. (2019). This area is characterized by heavy anthropic pressure: more than 60% of the landscape is represented by agricultural or urbanized territories (Zanin, 2022). The liver of one hare was not available in 2015 and therefore it was not considered in Stancampiano et al. (2019).

All organs were stored at −20 °C and thawed before examination. Gastrointestinal tract of one hare collected in 2013 was not available for gastrointestinal helminths collection. Gastrointestinal parasites were collected from gastrointestinal tract longitudinally opened, gently scraped with a microscope slide to allow the detaching of parasites and washed with tap water. The content, collected in conical flasks, was repeatedly washed to obtain the sediment to be screened under a stereomicroscope for parasite collection. Collected helminths were fixed in 70% ethanol solution with 5% glycerol. Nematodes were clarified and mounted in lactophenol, and identified using the key and description of Ransom (1911), Erickson (1944), Soulsby (1968), Gibbons and Khalil (1982), Anderson et al. (1983), Audebert et al. (2000) and Pinto et al. (2004). Lungs were macroscopically examined to find lesions caused by protostrongylids infections; trachea and bronchi were longitudinally opened. The heart, kidneys, liver, and peritoneum were macroscopically examined to highlight trematodes, cestode larvae or other helminth infections.

Representative samples from the available organs were collected, fixed in 10% buffered formalin at pH 7–7.6 for 24 h, embedded in paraffin wax, and five microns sections were stained with haematoxylin and eosin (H&E) for histological examination. Histological sections of tissues with the most interesting findings were photographed.

The Simpson's concentration index, an inverse measure of biodiversity measuring above all its evenness component (Keylock, 2005), was calculated using the prevalence (p) as index of importance of each parasite species as follows: $\Sigma\left(\frac{p}{\Sigma p}\right)^2$ (Holmes and Podesta, 1968; Guberti et al., 1993).

The statistical analyses (T-Student test, Chi-square test, Negative binomial regression) were performed using STATA 12.0. Significance threshold was set at $p < 0.05$.

3. Results

The total weight (in Kg), sex and age category of the examined hares during the two sampling periods are reported in Table 1. No significant differences were highlighted between the two periods.

The typical lung lesions caused by small strongyles infections were detected in 5.56% and 4.92% of hares in 2013 and 2015, respectively.

The prevalence of the parasites isolated is reported in Table 2. No intestinal cestodes were detected. Two nematode species, *Trichuris* sp. isolated from the intestine (only one female specimen in a single hare) and overall 16 specimens of *Micipsella numidica* isolated from the abdominal or thoracic cavity in 7 hares (Fig. 1), were detected in 2015 only.

Table 1
Comparison of average full weight, sex and age of the examined hare in the two sampling periods.

Year	Weight (sd)	Sex		Age[b]	
		male	female	adult	young
2013	3.38 (0.58)[a]	23	31	21	31
2015	3.37 (0.55)	27	34	23	37

Weight: Student-t = 0.08, p-value = 0.9364. Age: Chi-square = 0.05, p-value = 0.82. Sex: Chi-square = 0.032 p-value = 0.86. sd = standard deviation.
[a] Weight of one hare not available.
[b] The age was not available for 3 hares in 2013.

Table 2
Prevalence of the isolated parasites during the two sampling periods.

Year	2013	2015
Trichostrongylus retortaeformis	71.70%	70.50%
Taenia pisiformis	14.8%	3.3%
Trichuris sp.	0%	1.64%
Micipsella numidica	0%	11.4%

Fig. 1. *Micipsella numidica* (arrow) in the thoracic cavity of one hare.

Detailed results regarding the infection with *Taenia pisiformis* cysticerci are available in Stancampiano et al. (2019).

Simpson's concentration index calculated using parasite prevalence as measure of importance was 0.636 in 2013 and 0.610 in 2015. The same index calculated considering only gastrointestinal parasites was 1 in 2013 and 0.955 in 2015.

The intestinal nematode *Trichostrongylus retortaeformis*, with abundance and standard deviation (sd) of 22.15 (sd 41.49) and 54.89 (sd 110.80) in 2013 and 2015, was the dominant helminth species in both years.

Given the high variability highlighted by the large standard deviation, negative binomial regression models with constant terms only were built to evaluate the fitting with the negative binomial distribution and to estimate its k parameter, negatively related to parasite aggregation. The distribution was consistent with an aggregate distribution, significantly differing from a Poisson distribution in both sampling periods ($p < 0.001$); the estimated k parameters were 0.29 (confidence interval: 0.19–0.42) and 0.21 (c.i.: 0.15–0.30) in 2013 and 2015, respectively.

The results of the negative binomial regression model built to analyze the relationship between *T. retortaeformis* abundance and both host related parameters and sampling periods are reported in Table 3. In males and adults, *T. retortaeformis* abundance was significantly higher in 2015 and was positively related to host weight.

One *T. retortaeformis* male with an incomplete genital cone, lacking both *spicula* but with evident *gubernaculum*, was isolated from one hare hunted in 2013 (Fig. 2).

Macroscopic parasitic lesions in the lungs were characterized by multifocal, mildly raised greenish lesions surrounded by emphysematous lung tissue. Microscopical examination of the previously described lesion revealed foci characterized by adult nematodes and first stage larvae in the bronchioles and rare embryonated egg-in alveoli, with thickened bronchial and alveolar septa due to the inflammatory reaction. This picture was consistent with a verminous interstitial bronchopneumonia with desquamative alveolitis and multifocal infiltrates of lymphocytes, eosinophilic granulocytes, rare giant cells and isolated macrophages (Fig. 3). Emphysematous alveoli with thin walls surrounded the focal parasitic pneumonia.

In a single 2013 case the mildly raised focal greenish lesion was consistent with BALT hyperplasia and interstitial lymphocytic pneumonitis, without evidence of any parasitic form.

Only in hares hunted in 2013, focal lymphocytic infiltrates were occasionally detected in liver and heart without parasite infections; in addition, suppurative aspects in lungs and mediastinal lymph nodes were observed, in 2013, in one hare.

4. Discussion

The high prevalence of the intestinal nematode *T. retortaeformis* is consistent with previous findings in Italy and was frequently observed also in Europe (Shimalov, 2001; Chroust et al., 2012; Diakou et al., 2014; Kornaś et al., 2014; Sergi et al., 2018). *T. retortaeformis* confirms thus its adaptation and dominant position within the gastrointestinal helminth community of *Lepus europaeus*. However, to our best knowledge, most, if not all, European hare's gastrointestinal parasite communities comprise both two other nematodes, namely *Passalurus ambiguus* and *Graphidium strigosum* and cestodes belonging to the family Anoplocephalidae, such as *Andrya* sp., *Cittotaenia* sp. and *Mosgovoyia* sp. (Canestri Trotti et al., 1988; Poglayen et al., 1994; Shimalov, 2001; Chroust et al., 2012; Diakou et al., 2014; Kornaś et al., 2014; Sergi et al., 2018).

The presence of *Micipsella numidica* in 2015, serendipitously isolated for the first time in *L. europaeus* in Italy in the same area in 2013 by Gabrielli et al. (2016), is interesting from a parasitological and epidemiological point of view but probably insignificant as cause of disease, as no apparent lesion was associated with its presence. Its life cycle is still unknown, but its transmission is probably mediated by blood suckling dipterans with the role of active vectors similar to other filarial nematodes (Gabrielli et al., 2016). This nematode species has been reported in *Lepus granatensis* in Southern Spain by Segovia et al. (2014) who described a seasonal pattern of the infection. This seasonal pattern and the location of the parasite in abdominal or thoracic cavity and large blood vessels (the latter usually not examined during hare parasitological surveys) may be the causes of the paucity of reports in this host species, usually examined during the autumnal/winter hunting season.

Table 3
Results of the negative binomial regression model having *T. retortaeformis* abundance ad dependent variable. The term "ref" refers to the reference category of the dichotomous covariates.

		Coefficient	95% confidence interval		p-value
Year	2013	ref			
	2015	1.166	0.439	1.892	0.002
Sex	Male	ref			
	Female	−1.169	−1.970	−0.368	0.004
Age	Young	ref			
	Adult	1.488	0.526	2.451	0.002
Weight		0.918	0.055	1.781	0.037
Constant		−0.437	−3.277	2.404	0.763

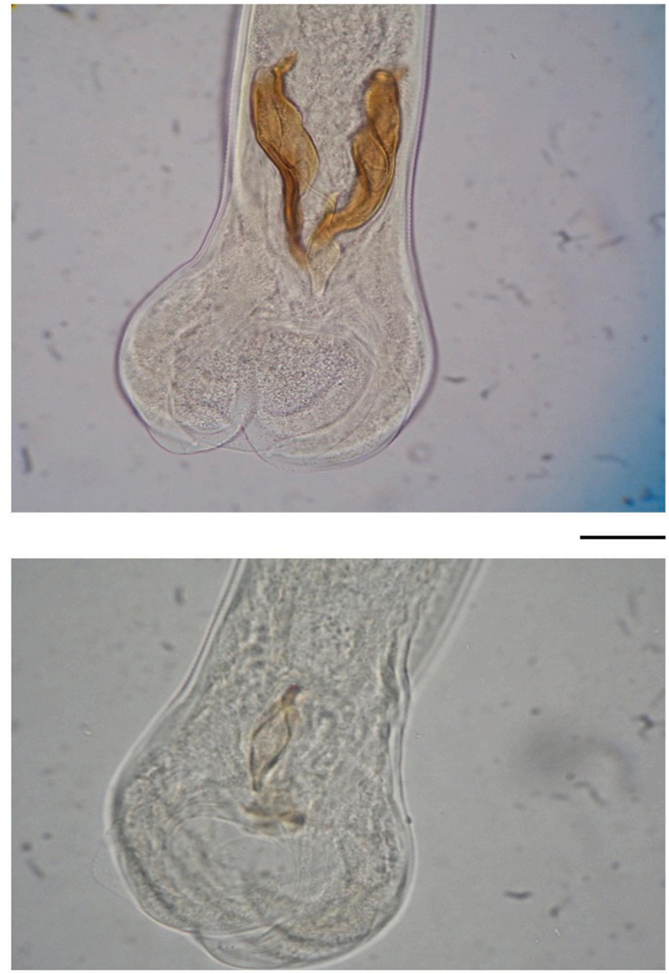

Fig. 2. Normal (up) and abnormal (bottom) *T. retortaeformis* male genital cone. In the abnormal nematode no *spicula* are present notwithstanding the perfectly developed *gubernaculum* (partially covered by the two spicules in the upper photo) and caudal bursa. Bar is 50 μm.

In our survey, the overall helminth richness was three species in 2013 (one in the gastrointestinal tract) and 5 in 2015 (two in the gastrointestinal tract). It indicates a very depauperate parasite biocoenosis, with few nematode species and no intestinal cestodes. The low parasite richness is not attributable to low sampling effort, the sample size of the present survey being comparable or larger than other similar Italian surveys looking for gastrointestinal helminths in hunted hares coming from the same area of the Emilia-Romagna Region (Poglayen et al., 1994) or in other areas of the same Region (Canestri Trotti et al., 1988). More specifically, Poglayen et al. (1994) examined 39 hares finding 2 nematode species and one cestode, while Canestri Trotti et al. (1988) found 3 nematodes and one cestode out of a sample of 82 hares and 2 nematodes and 3 cestodes out of another sample of 30 hares. The absence of intestinal cestodes in both years of the present survey is noteworthy. In addition to the low richness, also the low evenness is to be stressed: Simpson's concentration index had its maximum value (1)

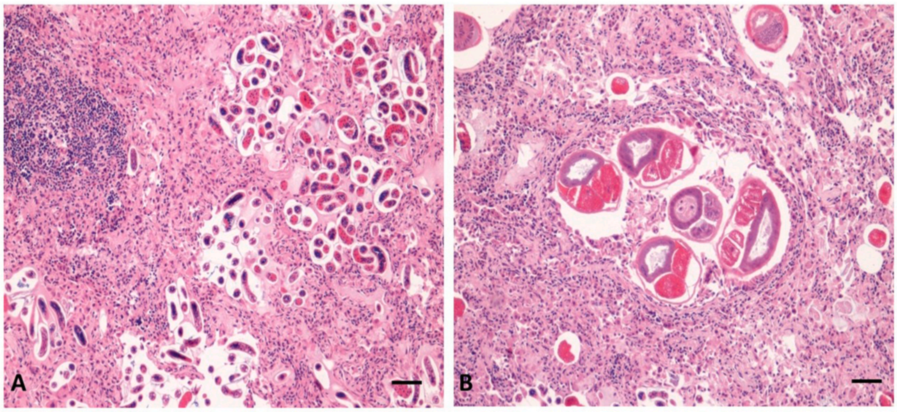

Fig. 3. Histological section of lungs of hares infected by *Protostrongylus* spp. A. Interstitial verminous bronchopneumonia with several cross and longitudinal sections of larvae on the right and the bottom of the photo. Bronchial and alveolar septa are thickened due to inflammatory cellular reaction (eosinophil granulocytes and mononuclear cells). A lymphoid nodule is visible on the left side. H&E, Bar = 100 μm. B. Interstitial verminous bronchopneumonia with scattered cross sections of adult parasites, five of them in the centre of the photo. H&E, Bar = 100 μm.

in 2013, representing the smaller biodiversity (only one species dominate the gastrointestinal helminth communities); it appeared just a little improved in 2015 reaching the value 0.955. The same index calculated from the data published in the similar Italian surveys reported above gives 0.668 and 0.509 in the samples of Canestri Trotti et al. (1988) and 0.680 in the sample of Poglayen et al. (1994), both showing higher biodiversity than the present survey.

Parasitism, both "true" and protelean, has independently evolved in 15 out of 35 major animal phyla and currently represents the 41% of known metazoan biodiversity; despite parasites' high coverage of animal kingdom, their role in food webs and their regulatory function in ecosystems, they represent a "ghost biodiversity" which, up to now, has poorly been surveyed and thus less understood (Gómez and Nichols, 2013).

In this survey the loss of parasite species is evident, and the possibility that hare intestinal cestodes have been locally extinct is far from simply hypothetical. Human harvesting and agricultural pollution may have had a role: according to Budria and Candolin (2014) human disturbance is likely to have more impact on parasites with indirect cycle, such as cestodes; in particular intestinal cestodes belonging to the Family Anoplocephalidae are known to have free-living oribatid mites as intermediate host, that would therefore have been particularly influenced by chemicals used in the agricultural area of the present survey or by other environmental factors.

A hypothetical influence of pollution directly acting on monoxenous parasites, such as *T. retortaeformis*, is coyly suggested by the specimen with missed spicules observed in one hare. Abnormal spicule development is reported very sporadically in literature (Becklund, 1960; Andews, 1970; Roy and Beveridge, 1997; Gibbons et al., 2000) and to our best knowledge the total absence of spicules has never been reported. The abnormal development reported by Becklund (1960) occurred more frequently in worms exposed to phenothiazine, therefore sustaining our hypothesis.

The results clearly suggest that hare parasites (with the possible exception of *T. pisiformis*, as detailed in Stancampiano et al., 2019) are far from being a threat to their host, probably dealing, on the contrary, with the same external negative pressures. Actually, the dominant helminth, *T. retortaeformis*, is more abundant in individuals with higher weight, that is consistent with little or no harm both at the host individual and population level.

Also, pathological findings are primarily unrelated to parasitism; although histological findings were consistent with the diagnosis of focal-multifocal verminous bronchopneumonia caused by adults and larvae of *Protostrongylus* spp., other lesions (i.e., suppurative), detected interestingly in 2013 only, mainly were related to bacterial infection of unknown origin. Anecdotally, the abnormally developed *T. retortaeformis* male was isolated just in 2013. It is probable that the same factors giving rise to host decline also endangered parasite populations, directly or using host density reduction. For example, Prüter et al. (2018) found a relationship between lead intoxication and the decrease of intestinal helminth species richness in mallards. The low helminth diversity (coupled to pathological lesions) is particularly evident in the first year of this survey, consistently with the possible tendency toward host-parasite equilibrium suspected by Stancampiano et al. (2019). A tendency toward hare population recovery is barely observable from the recent data collected from hunter associations (Zanin, 2022); hunting and capture activity reduction have possibly promoted this recovery and the observed slow improvement of parasite biodiversity.

In conclusion, our results suggest that the conservation of hosts, environment, and parasites can not be achieved separately and that parasites and wildlife hosts' destinies are intimately linked, confirming the complexity of ecosystems and the need to contemplate parasite biodiversity in conservation strategies.

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Declaration of competing interest

None.

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