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Review Article

Helminth parasites of wolves (*Canis lupus*): a species list and an analysis of published prevalence studies in Nearctic and Palaearctic populations

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Abstract

A literature survey was undertaken in order to draw up a definitive list of helminth parasites of the wolf, *Canis lupus*. From 27 papers a total of 72 helminth species from 40 genera were recorded that infect wolves, of which 93% were identified from the gastrointestinal tract at necropsy. They comprised 28 species of nematode, 27 species of cestode, 16 species of trematode and one acanthocephalan. Of these, 46 species were able to be included in further meta-analysis of prevalence data derived from 25 publications for which the total number of wolves examined was 1282 (1066 from Nearctic populations, and 216 from the Palaearctic region). These two populations were further subdivided into three relevent ecosystems or biomes, i.e. temperate/montane ($n = 216$), boreal ($n = 805$) or tundra ($n = 261$). The meta-analysis of relative prevalence indicated the most common helminth species to be the tapeworm *Taenia hydatigena*, which occurred at relative rates of >30% for either zoogeographic region as well as in each of the three biomes. The related tapeworm, *Echinococcus granulosus* also exhibited high meta-prevalence (>19%) in all host biomes. The hookworm *Uncinaria stenocephala* was the most prevalent nematode species by meta-analysis (meta-prevalence 44.9%) in the temperate/montane biome, while the ascarid *Toxascaris leonina* was the dominant helminth species (meta-prevalence 73.9%) in the tundra wolf populations. Trematodes in the genus *Alaria* were the dominant fluke (meta-prevalence 3–5%) in all biomes. Analysis of published studies for helminth biodiversity using the Shannon-Wiener index based on species number and meta-prevalence by region or biome, indicated that highest helminth diversity occurred in wolf populations of the temperate/montane biome (Palaearctic), and was lowest in tundra wolf populations of the Nearctic ($P < 0.05$). Helminth species assemblage in European wolf populations was therefore at least as great or more varied than was recorded for the larger less disturbed wolf populations of North America.

Introduction

The wolf (*Canis lupus*) is the largest extant member of the family Canidae, with males up to 75 kg. Most live in packs of extended family units of 5–12 members,

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with pack size also dependent on the availability of prey, so that groups of 20–30 animals are not uncommon where prey is abundant (Mech, 1970). Pack territory varies from 65–300 km^2. Though formerly widely distributed over the whole Nearctic and Palaearctic regions, significant wolf populations are currently mainly confined to the Holarctic, especially of Canada (30,000–60,000 animals) and Russia (50,000–100,000), although sustainable populations (>2000 animals) also occur in parts of Central Asia including Mongolia, north-west China, Kazakhstan, and Alaska (Nowak, 1999). Wolf populations in the contiguous states of USA are small and vulnerable, but populations appear to be increasing especially in Wisconsin, Minnesota and Michigan (approximately 4000 in total) (Treves *et al.*, 2004). Translocation programmes have also been successful in re-introducing wolves into the Yellowstone Park ecosystem (Hampton, 1997). In continental Europe populations of wolves are highly fragmented with highest densities in wilderness areas of the eastern European countries of Romania, Poland and Belarus (Mituch *et al.*, 1994; Shimalov & Shimalov, 2000). Estimated numbers of wolves in western Europe are 2500–3000, with most located in north-west Spain (Cuesta *et al.*, 1991; Segovia *et al.*, 2001). Wolf conservation programmes have also tried to protect smaller populations in the Appenines of Italy, the Mercatour National Park in south-west France, and in parts of Scandinavia especially Norway and Finland (Guberti *et al.*, 1993; Hirvela-Koski *et al.*, 2003). Within the wolf range over North America (including Greenland) and eastern/western Europe the three main biomes that can sustain populations broadly fall into the categories of tundra (arctic), boreal (subarctic and lower latitudes) and mixed montane (temperate mixed forest) (Custer & Pence, 1981).

Prey species of wolves may vary from fish, amphibians, reptiles, birds and small mammals to large ungulates, with prey selection dependent on availability and ease of predation (Nowak, 1999). It is not surprising therefore that the helminth parasite fauna of *Canis lupus* is relatively large, and parasite species may also vary markedly, dependent on prey species, wolf biome and probably also zoogeographical region as a reflection of prey species biodiversity and their relative population densities (Holmes & Podesta, 1968; Guberti *et al.*, 1993). Those gastrointestinal helminth parasites with indirect life-cycles that incorporate one or more intermediate hosts should be expected to be relatively common in a top predator such as the wolf because of natural selection for trophic transmission pathways and asexual multiplication in larval stages (Combes, 2001; Trouve *et al.*, 2003). Wolf predator–prey interactions will therefore tend to favour transmission of cestode and trematode species, e.g. *Taenia* spp. or *Alaria* spp. respectively, but also for nematode species with indirect cycles, e.g. *Trichinella* spp. (Holmes & Podesta, 1968; Guberti *et al.*, 1993; Pozio *et al.*, 2001). Directly transmitted nematode species also infect wolves especially where contamination of den or toilet areas occurs, e.g. for hookworms of *Uncinaria* spp. (Mech, 1970).

Parasites and infections of wolves have previously been broadly reviewed (Erickson, 1944; Mech, 1970), and several specific studies on helminths of wolves have been published, especially for wolf populations in Canada (e.g. Freeman *et al.*, 1961; Choquette *et al.*, 1973), USA (e.g. Rausch & Williamson, 1959; Byman *et al.*, 1977), Spain (Segovia *et al.*, 2001) and Italy (Guberti *et al.*, 1993). However, a comprehensive list of helminth parasites of *C. lupus* has not been published. Furthermore, relatively little comparative data is available for helminth fauna of North American vs. European wolf populations, or for the major wolf biomes that comprise temperate/montane, boreal or tundra ecosystems (Holmes & Podesta, 1968; Custer & Pence, 1981; Guberti *et al.*, 1993).

With a view to the future application of copro-antigen or copro-PCR tests (Jenkins *et al.*, 2000; Abbasi *et al.*, 2003) to survey selected wolf populations for the taeniid cestode *Echinococcus granulosus*, we have initially undertaken a review of the published literature on helminth parasites of wolves in order to draw up a definitive species list. An additional aim of this review was to analyse published studies in order to compare the relative prevalence and biodiversity indices of gastrointestinal helminth parasites of *C. lupus* in relation to both zoogeographical region (Nearctic vs. Palaearctic) and to resident biome (tundra, boreal, or temperate/montane).

Methods

A search of literature on wolf helminths was carried out up to early 2004. Papers published in English or with an English abstract were prioritized. A list of all helminth species recorded by scientific name was drawn up. The list was derived from studies that involved necropsy with gut examination ($n = 16$), partial necropsy report, e.g. muscle examination ($n = 5$), and/or coproparasitological analysis ($n = 9$) (table 1). In addition, some studies involved immunodiagnostic testing of wolf scats using an *Echinococcus* coproantigen ELISA (Jenkins *et al.*, 2000), $n = 4$, includes three unpublished studies by the author P.S. Craig) (table 1). In addition to helminth species, the site of parasitism (mainly intestinal), likely intermediate host(s), and geographic location were also noted. Published studies with quantitative data on prevalence and/or intensity data of helminth species were selected by biome and zoogeographic region for a comparative meta-analysis. Spreadsheets were used to store extracted data (mostly prevalence) and arranged to compare helminth species of wolf populations sampled in three biomes, i.e. tundra, boreal or temperate montane. A general comparison was also made of helminth fauna from wolf populations in the Nearctic vs. the Palaearctic region. Prevalence rates for helminths were calculated by combining individual data sets for each biome (meta--prevalence).

Statistical analysis

Biome level (tundra vs. boreal vs. temperate/montane) prevalence for a helminth species was calculated simplistically as the total proportion infected from the total wolf numbers combined from each relevant published study. When a study did not specifically state the actual numbers (n) of wolves infected with a particular helminth the stated prevalence (%) was used

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Table 1. Selected studies on helminths of wolves by region or country, whether necropsy or faecal examination was carried out (*n* wolves, or samples) and the respective author reference.

	Study	Author	*n*	Type of study
1	SW Quebec, Canada	McNeil *et al.*, 1984	25	Necropsy and faecal
2	Yukon, Canada	Choquette *et al.*, 1973	182	Necropsy
3	Ontario, Canada	Freeman *et al.*, 1961	520	Necropsy
4	SW Manitoba, Canada	Samuel *et al.*, 1978	12	Necropsy
5	Canada	Sweatman, 1952	58	*E. granulosus* only
6	Alberta, Canada	Holmes & Podesta, 1968	98	Necropsy
7	Alaska, USA	Zarnke *et al.*, 1999	148	*Trichinella* spp. only
8	Alaska, USA	Rausch & Williamson, 1959	200	Necropsy
9	NE Minnesota, USA	Byman *et al.*, 1977	204	Scats/faeces
10	Minnesota, USA	Riley, 1939	12	*E. granulosus* only
11	Minnesota, USA	Erickson, 1944	18	Necropsy
12	Wisconsin, USA	Archer *et al.*, 1986	71	Scats/faeces
13	Yellowstone N.P., USA	Storandt & Craig, unpublished	37	Scats, echino-copAg
14	Isle Royale (Michigan), USA	Peterson & Craig, unpublished	70	Scats, echino-copAg
15	Greenland	Marquard-Peterson, 1997	423	Scats/faecal
16	Spain	Torres *et al.*, 1996	22	Necropsy
17	NW Spain	Segovia *et al.*, 2001	47	Necropsy
18	Greece	Papadopoulos *et al.*, 1997	6	Necropsy
19	Italy	Pozio *et al.*, 1996	81	*Trichinella* spp.
20	Italy	Stancampino *et al.*, 1994	48	*Trichinella* spp.
21	Italy	Guberti *et al.*, 1993	89	Necropsy
22	Germany	Priemer *et al.*, 2002	2	Necropsy
23	France	Giraudoux & Craig, unpublished	95	Scats
24	Finland	Oivanen *et al.*, 2002	18	*Trichinella* spp.
25	Finland	Hirvela-Koski *et al.*, 2003	23	Necropsy, echino-copAg
26	Slovakia	Martinek *et al.*, 2001	23	E.multi cop-PCR
27	Belarus	Shimalov & Shimalov, 2000	52	Necropsy
28	Russia	Pozio *et al.*, 2001	82	*Trichinella* spp.
29	China	Tang *et al.*, 2004	6	Necropsy (*E. granulosus*)

echino-copAg, *Echinococcus granulosus* coproantigen ELISA after Craig *et al.*, 1995; E.multi cop-PCR, coproPCR for *E. multilocularis.*

to back-calculate the number infected. Those studies that reported only on individual helminth infections (e.g. *Trichinella* in muscle biopsy, or *Echinococcus* coproantigen positives), or only involved faecal analysis, were not included in the meta-analysis.

A wolf helminth biodiversity index calculation (Magurran, 1988) for a particular biome or region was estimated using overall prevalence values for each helminth species rather than intensity (the preferred value) because of limited published data (Holmes & Podesta, 1968; Guberti *et al.*, 1993). Species diversity was based on the Shannon-Wiener index and used to compare helminth diversity at biome level, i.e. tundra vs. boreal vs. temperate montane, and by zoogeographical region, i.e. Palaearctic vs. Nearctic (Magurran, 1988; Fowler & Cohen, 1992).

Results

A total of 27 papers relating to parasites of wolves (*C. lupus*) were identified, of which 25 contained usable helminth data sets. These studies, published between 1939 and 2004, related to wolf population samples (range $n = 2–520$) from Canada, USA (contiguous states and Alaska), Russia, Belarus, Slovakia, Italy, Spain, Greece, France, Finland and China (see tables 1 and 2). A total of 72 helminth species from 40 genera were recorded (93% from the intestinal tract), comprising 27 species of cestode from nine genera, 16 species of trematode from ten genera, 28 species of nematode from 20 genera, and one species of acanthocephalan (table 2).

The two most prevalent gastrointestinal helminth species of wolves in all studies were the hookworm *Uncinaria stenocephala* (individual study range 2.5–67%) and the tapeworm *Taenia hydatigena* (range 4–79%). The most prevalent trematode species were the intestinal flukes *Alaria alata* and *A. americana* (range 2–11%). Records for the tissue stage of *Trichinella* showed a prevalence range of 12.8–97.5%. Overall, the most common helminth genus parasitizing wolves was *Taenia* with 13 species recorded, followed by *Alaria* with six species recorded. Perhaps unsurprisingly, those helminth species (typified by taeniids) which are transmitted by predation on mammalian hosts such as ungulates, lagomorphs or rodents were the most commonly recorded in wolves (approximately 40% of helminth species). Helminth species were also transmitted as a result of wolf predation on reptiles and amphibians (e.g. *Reticularia* spp. and *Dioctophyma renale*), also from fish (e.g. *Diphyllobothrium latum* and *Opisthorchis felineus*), and ingestion of crustaceans (e.g. *Paragonimus westermanii*) or earthworms (*Pearsonema plica*). Direct life-cycle transmission occurred for at least five species of gastrointestinal nematodes (table 2).

Table 2. List of helminth species recorded from wolves at necropsy, indicating host site, intermediale host type, geographic location and reference.

	Site*	Intermediate host(s)	Geographic location (Reference**)
Cestodes			
Diphyllobothrium latum	SI	Fish	Canada (13), Russia (9)
Diplopylidium nolleri	SI	Lizard (paratenic)	Russia (9)
Dipylidium caninum	SI	Flea, lice	E. Europe (9, 23)
Echinococcus granulosus	SI	Moose, cervids	US (4), Can (8, 13), Europe (6, 7, 23), China (25)
Echinococcus multilocularis	SI	Voles	Russia (9, 13), E. Europe (23)
Joyeuxiella echinorhynchoides	SI	Arthropods, reptiles (paratenic)	Greece (15)
Joyeuxiella pasqualei	SI	Lice, fleas	Europe, Asia, Russia (13)
Joyeuxiella rossicum	SI	Arthropods, reptiles (paratenic)	Russia (9)
Mesocestoides kirbyi	SI	Arthropods, small vertebrates	Canada (3), W. Europe (15, 22, 26)
Mesocestoides lineatus	SI	Mites, small vertebrates	W. Europe (6, 26), E. Europe (23), Russia (9)
Multiceps packii	SI	Hare, rabbit	Russia (13), US (4)
Spirometra erinacei	SI	Crustacean, amphibians, mammals	E. Europe (23), Asia (13)
Spirometra janickii	SI	Arthropods, terrestrial vertebrates	Europe (13)
Taenia crassiceps	SI	Rodents	Canada (13, 21), E. Europe (13, 23), Russia (9)
Taenia hydatigena	SI	Cervids, large vertebrates	US (4), Alaska (19), Europe (6, 26), Canada (3, 5,12)
Taenia (ovis) krabbei	SI	Moose, deer	Russia (9, 13), Alaska (19), Canada (3, 13), E. Europe (23)
Taenia laticollis	SI	Lagomorphs	Canada (13)
Taenia macrocystis	L, T	Squirrel, lagomorphs	Russia (13)
Taenia multiceps	SI	Snowshoe hare, lagomorphs	US, Canada, Russia (13), W. Europe (6, 26)
Taenia (multiceps) skrjabini	SI	Sheep, goats	Russia (13)
Taenia omissa	SI	Deer	Canada (13)
Taenia ovis ovis	SI	Sheep, cervids	Italy (6)
Taenia parenchimatosa	SI	Reindeer, red deer	Russia (9, 13)
Taenia pisiformis	SI	Arctic hare, rabbit	US, Canada, Russia (3, 13), Europe (6, 23, 26)
Taenia polyacantha	SI	Rodents	Russia (9, 13), E. Europe (23)
Taenia serialis	SI	Hare, rabbit	Russia (9, 13), Spain (22), Canada (3)
Taenia taeniaeformis	SI	Rodents	Canada (13)
Trematodes			
Alaria alata	SI, ST	Snail, frog, fish, rodents, mink	Russia, Asia (13, 23), W. Europe (22,26), US (1)
Alaria americana	SI	Snail, frog, rodents	Canada (3, 8, 12, 13, 21)
Alaria arisaemoides	SI	Snail, frog	Canada (3, 8, 21)
Alaria canis	SI	Snail, frog, rodents	Canada (13, 12), Alaska (19)
Alaria marcianae	SI	Snail, frog, rodents	Canada (12, 21)
Alaria metorchis	L	Snail, frog, rodents	US (13)
Clonorchis sinensis	L	Snail, fish	Russia (9)
Heterophyes heterophyes	SI	Snail, fish	Not stated (13)
Heterophyes persica	SI	Snail, fish	Europe, Asia (13)
Isthmiophora melis	SI	Snail, amphibian, fish	Belarus (23), Russia (9)
Metagonimus yogakawi	SI	Snail, fish	Asia (13)
Metorchis conjunctus	SI	Snail, fish	Canada (8)
Nanophyetus salmincola	L	Snail, fish	Russia (9)
Opisthorchis felineus	L	Snail, fish	Belarus (23)
Paragonimus westermanii	LG	Snail, crayfish, crab	Korea (13)
Pseudamphistomum truncatum	GB	Fish	Belarus (23), Russia (9)
Nematodes			
Ancylostoma braziliense	SI	Direct	Asia (13)
Ancylostoma caninum	SI	Direct	Asia, Russia (13), Europe (6, 22, 26), E. Europe (23)
Angiostrongylus vasorum	CVS	Frog, fish, mink	W. Europe (22, 26)
Capillaria plica	BL	Direct or earthworms	Belarus (23)
Crenosoma vulpis	LG	Slugs and snails	Europe, Russia (13, 23)
Dioctophyma renale	K	Frogs, fish	US, Europe, Asia (13), Canada (12)
Dirofilaria immitis	SI, H	Mosquito	Spain (22)
Dirofilaria repens	SC	Mosquito	Asia, Russia (9, 13)
Eucoleus (Capillaria) aerophilus	LG	Direct or rodents	Canada (8), Russia (13), US (1, 2)
Filaroides (Oslerus) osleri	LG	Snails	US (2, 4), Canada (21)
Metathelazia petrovi	LG	Molluscs (paratenic)	Russia (9)
Nematodirus helvetianus	SI	Direct	Greenland (10)
Onchocerca lupi	SC	Blackfly	Russia (9)
Pearsonema plica	BL	Earthworm	W. Europe (22, 26)
Physaloptera rara	ST	Direct or rodents	US (13)
Physaloptera sibirica	ST	Direct or rodents	Russia (13)

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Table 2. *continued.*

	Site*	Intermediate host(s)	Geographic location (Reference**)
Reticularia affinis	SI	Reptiles	Russia (13)
Reticularia cahirensis	SI	Reptiles	Russia (13)
Reticularia lupi	SI	Reptiles	Russia (13)
Reticularia spp.	SI	Reptiles	Greece (15)
Spirocerca arctica	ST, SI, T	Beetles, terrestrial vertebrates	Canada (3)
Spirocerca lupi	ST, SI, T	Beetles, terrestrial vertebrates	Canada (3), E. Europe (23)
Toxascaris leonina	SI	Rodents	Canada (3, 13, 21), Alaska (13), Russia (13, 23), Greenland (10)
Toxocara canis	SI	Direct	Canada, US (2, 8, 13), Europe (6, 15, 22, 23, 26)
Toxocara mystax	SI	Direct	Europe, Asia (13)
Trichinella britovi	SI, M	Range of mammals	Italy (24)
Trichinella spiralis	SI, M	Range of mammals	Alaska (19,20,27), Russia (18), Europe (14, 17)
Trichuris vulpis	LI	Direct	Asia (13), Europe (6, 22, 23, 26), US (2, 16)
Uncinaria stenocephala	SI	Direct	Canada (2, 8), Alaska (19), Russia (13), Europe (6), Greenland (10)
Acanthocephala			
Macroacanthorynchus catulinus	SI	Beetles	Belarus (23)

* BL, bladder; CVS, cardiovascular system; GB, gall bladder; H, heart; K, kidneys; L, liver; LG, lungs; LI, large intestine; M, muscle; SC, subcutaneous; SI, small intestine; ST, stomach; T, tissues.

** (1) Archer *et al.*, 1986; (2) Byman *et al.*, 1977; (3) Choquette *et al.*, 1973; (4) Erickson, 1944; (5) Freeman *et al.*, 1961; (6) Guberti *et al.*, 1993; (7) Hirvela-Koski *et al.*, 2003; (8) Holmes & Podesta, 1968; (9) Kozlov, 1977; (10) Marquard-Peterson, 1997; (11) Martinek *et al.*, 2001; (12) McNeil *et al.*, 1984; (13) Mech, 1970; (14) Oivanen *et al.*, 2002; (15) Papadopoulos *et al.*, 1997; (16) Peterson & Craig–faecal analysis, unpublished; (17) Pozio *et al.*, 1996; (18) Pozio *et al.*, 2001; (19) Rausch & Williamson, 1959; (20) Rausch *et al.*, 1956; (21) Samuel *et al.*, 1978; (22) Segovia *et al.*, 2001; (23) Shimalov & Shimalov, 2000; (24) Stancampino *et al.*, 1994; (25) Tang *et al.*, 2004; (26) Torres *et al.*, 1996; (27)

Wolf biome and helminths

Parasitological studies on wolf populations were divided into three host ecosystems or biomes for a meta-analysis of relative prevalence of helminth species. A total of 1282 wolves identified from studies were subdivided into a temperate/montane biome ($n = 216$), a boreal biome ($n = 805$) and a tundra biome ($n = 261$). In total, 19 tapeworm species, seven trematode species and 20 nematode species were included in the wolf biome study. Meta-prevalence calculations were summarized for the more common species where a combined prevalence was calculated to be >5% in the montane temperate biome (table 3). In that biome, typified by the mountain ranges of north-west Spain and central northern Italy, the most prevalent helminth was the nematode *Uncinaria stenocephala* (a meta-prevalence of 44.9%) with *Taenia hydatigena* also highly prevalent (38.4%). In the boreal or northern forest zone, typified by parts of Alberta and southern Alaska, the cestode *T. hydatigena* was most prevalent with an estimated combined prevalence of 42%, with another taeniid cestode, *Echinococcus granulosus*, the second commonest helminth species infecting wolves (meta-prevalence 28.2%). Wolf populations in the tundra zone, typified by northern Alaska and Greenland, were highly parasitized by the ascarid *Toxascaris leonina* (meta-prevalence of 73.9%) as well as the two taeniid species *Taenia krabbei* and *T. hydatigena* both with >30% prevalence. Large ungulates are the intermediate hosts for these latter two *Taenia* species. In fact, tapeworms in the family Taeniidae were the most prevalent group across all three biomes, including *E. granulosus* which had a meta-prevalence >19% (table 3) and where individual study prevalences ranged from 11.5 to 83% (data not shown). The tapeworm *T. multiceps*, which like *E. granulosus* also reproduces asexually as a tissue dwelling larval cyst in ungulates, had a greater overall prevalence (14.4%) in wolves residing in the European temperate/montane biome, but did not occur or was of negligible occurrence (overall 0.2%) in the North American boreal or tundra zones. Similarly, trematode species in the genus *Alaria* generally exhibited a low overall prevalence reaching >5% only for *A. alata* in the temperate/montane biome (table 3). The muscle encysted larvae of the nematode *Trichinella spiralis* were recorded in 20.6% of wolves sampled in the temperate/montane biome with a similar prevalence (19.2%) for wolves from the tundra biome, but was not recorded from wolves sampled in the boreal forests of North America. However, fewer tissue biopsy studies were undertaken in the North American studies. Data on helminth species intensity in wolves was generally lacking in the literature, but was reported for a few European studies. The mean burden of *T. hydatigena* ranged from 1 to 30 tapeworms, for *U. stenocephala* the range was 30–61 worms and for *Toxascaris* was 2–8 worms (Guberti *et al.*, 1993; Shimalov & Shimalov, 2000; Segovia *et al.*, 2001).

Zoogeographical region and wolf helminths

Of the three biomes, the temperate/montane regions of Europe and Russia (Palaearctic region) had more records of helminth species (35 species) compared to the boreal (22 species) or tundra zones (11 species) of North America (Nearctic region). The most prevalent helminth species recorded (40%) in the Nearctic region was the tapeworm *T. hydatigena* which uses ungulates as intermediate host, and it was also highly prevalent in the Palaearctic populations (41.7%). The gut nematode *U. stenocephala* was the most prevalent helminth (44.9%) in wolves

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Table 3. Relative meta-prevalence (%) of selected species of wolf helminths in different host biomes (boreal, montane, tundra) determined by combining prevalence studies for each biome.

Helminth	Montane	Boreal	Tundra
Alaria alata	5.1		
Alaria americana		1.9	
Alaria canis			3.7
Alaria marcianae		0.6	
Ancylostoma caninum	12		
Capillaria spp.			0.002
Diphyllobothrium spp.		0.1	0.4
Dipylidium caninum	7.4		
Echinococcus granulosus	19.4	28.2	23
Taenia crassiceps		0.7	
Taenia hydatigena	38.4	42.9	31
Taenia krabbei	6.5	25	33.7
Taenia laticollis		1.0	
Taenia multiceps	14.4		
Taenia pisiformis	5.5	6.8	
Taenia serialis		5.1	3.8
Toxascaris leonina	6.5	12	73.9
Toxocara canis	9.7	0.1	
Trichinella spiralis	20.6		19.2
Trichuris vulpis	7.4		
Uncinaria stenocephala	44.9	2.1	5.4

sampled from the Palaearctic sites. The taeniid tapeworm species *E. granulosus* was twice as commonly recorded in the Nearctic (31% vs. 14%), while another taeniid, *T. krabbei* had a meta-prevalence of only 6.5% in the Palaearctic region but was the third most prevalent helminth (27.2%) in the Nearctic. The small gut fluke *A. alata* was the only trematode species with >3% overall prevalence in wolves for both Nearctic and Palaearctic regions (table 4).

Helminth species diversity in wolves

The number of helminth species recorded in wolf populations decreased with increasing latitude with the smallest species assemblage recorded in the tundra biome. The Shannon-Wiener index (SWI) was used to measure helminth species diversity (Magurran, 1988) for the published studies ($n = 25$) where data was available for the three biomes and the two zoogeographic regions. Helminth biodiversity was highest (SWI = 2.74) for the temperate montane forest wolf populations and lowest (SWI = 1.73) in the tundra biome host populations. The SWIs were significantly different between the three biomes ($P < 0.05$) (table 5). Calculation of the Shannon--Wiener index for helminth species diversity in wolf populations from the Nearctic vs. the Palaearctic region indicated significantly greater diversity in the Palaearctic populations (table 6). It should be noted that these are crude estimates of biodiversity because they are based on combined prevalence calculations for different studies rather than species intensity, and in addition sampling strategies will have varied between individual studies.

Table 4. Relative meta-prevalence (%) of selected helminth species of wolves in the Nearctic ($n = 1066$) and Palaearctic ($n = 216$) regions by meta-analysis of 25 prevalence studies.

Helminth	Nearctic	Palaearctic
Alaria alata	3.9	5.1
Capillaria plica	0.2	0.3
Crenosoma vulpis		7.7
Dioctophyma renale	0.5	
Echinococcus granulosus	31	14.1
Taenia hydatigena	40	41.7
Taenia krabbei	27.2	6.5
Taenia multiceps	0.2	14.4
Taenia pisiformis	5.2	5.5
Taenia serialis	4.8	6.5
Toxascaris leonina	27.2	9.7
Toxocara canis	0.5	35.7
Trichinella spiralis	4.8	7.4
Uncinaria stenocephala	2.9	44.9

Discussion

The literature survey identified a total of 72 species of helminth parasite recorded from wild wolves (*Canis lupus*) associated with 27 publications published between 1944 and 2004. These comprised 28 nematode species, 27 cestode species, 16 trematode species and one species of acanthocephalan. This represents the most comprehensive list of helminths of wolves that have been collated to date. The list of species is impressive and reflects long standing host-parasite relationships, which are dominated by gastrointestinal helminths (93%) that exhibit indirect life-cycles inolving predation on, or ingestion of, a wide range of vertebrates (mammals, reptiles, amphibians and fish) and also invertebrates (arthropods, annelids). The two most prevalent gastrointestinal helminth parasites of wolves recorded in individual studies were the tapeworm *Taenia hydatigena* (range 4–79%) which is transmitted trophically between wolves and large ungulates, and the direct life-cycle nematode *Uncinaria stenocephala* (range 2.5–67%).

In order to compare prevalence of the commoner helminth species between host biome (montane/temperate, boreal forest, or tundra) or zoogeographic region (Palaearctic or Nearctic), a meta-analysis of prevalence data for a selected number of published wolf helminth studies ($n = 25$) was undertaken which included a total sample of 1282 wolves. *Taenia hydatigena* was clearly the most prevalent tapeworm of wolves in boreal (38.4%) and temperate/montane (32.9%) biomes, and second only to *T. krabbei* (31%) in

Table 5. Shannon-Wiener index (SWI) as a crude measure of helminth species diversity in montane, boreal and tundra biomes.

	Montane	Boreal	Tundra
No. species	36	22	11
No. individuals	499	1028	508
SWI	2.735*	1.826*	1.726

$P < 0.05$, montane* vs. boreal/tundra, boreal* vs. tundra.

Table 6. Shannon-Wiener index as a crude measure for helminth species diversity in Nearctic and Palaearctic zoogeographical regions.

	Nearctic	Palaearctic
No. species	33	37
No. individuals	1066	216
SWI	2.24	2.83*

$P < 0.05$, Palaearctic* vs. Nearctic.

the arctic tundra biome. In Spanish wolf populations, which are the largest in western Europe, the most prevalent species were again *T. hydatigena* (44.7%) and the hookworm *U. stenocephala* (51.1%), and both these parasites have also been recovered from domestic dogs and red foxes (*Vulpes vulpes*) on the Iberian peninsula (Segovia *et al.*, 2001). The other hookworm species *Ancylostoma caninum* had an overall prevalence of 12% in the Palaearctic wolf populations but was not reported in any of the North American necropsy studies, and this is probably due to larval transmission being adapted to warmer climes of more southern latitudes (Custer & Pence, 1981; Stancampino *et al.*, 1994). The gut and tissue dwelling nematode *Trichinella* was prevalent (~20% overall) when sampled in both tundra and montane biomes, though was not reported from studies on boreal wolf populations in North America. Transmission of *Trichinella* is through predation, scavenging or cannabalism and allows the parasite to adapt to a wide range of hosts and ecosystems including the Arctic (Rausch *et al.*, 1956; Pozio *et al.*, 2001).

A high overall prevalence (28.2%) for the potentially zoonotic taeniid, *Echinococcus granulosus* (Craig *et al.*, 2003) was calculated from individual studies in the boreal zone of North America and only *T. hydatigena* was more prevalent in that biome. In northern USA and Canada, *E. granulosus* is maintained in a sylvatic predator–prey transmission cycle between wolves and primarily moose (*Alces alces*) (Choquette *et al.*, 1973; Messier *et al.*, 1989), but also caribou (*Rangifer tarandus*) in northern Canada and Alaska (Rausch, 2003). Severe pulmonary infections with hydatid cysts of *E. granulosus* occur in aged moose whose vital capacity and stamina will be decreased and as a result may be preferentially predated on by wolves (Messier *et al.*, 1989). Other taeniids transmitted to wolves in North America via predation on large ungulates include *T. hydatigena* and *T. krabbei*. The overall meta-prevalence of *T. krabbei* in the boreal region was calculated at 25% compared to 33.7% in the tundra biome, but was reversed for *T. hydatigena* (i.e. 42.9% in boreal vs. 31% in tundra). Higher prevalence of *T. krabbei* in tundra wolves was also reported by Choquette *et al.* (1973). This difference is probably due to the wider range of intermediate host species for *T. hydatigena* (i.e. cervids, bovids, caprids), while *T. krabbei* appears to be restricted to deer (cervids) intermediate hosts with caribou as a predominate prey species in Nearctic tundra zones (Jones & Pybus, 2001; Rausch, 2003). Other taeniids such as *T. pisiformis* and *T. serialis* reflect lagomorph prey in wolf diets but these species never exceeded an overall meta-prevalence of 5% in any biome, although in one single study in the Yukon where the main intermediate host is the snowshoe hare (*Lepus americanus*), 57% of wolves harboured *T. serialis* (Choquette *et al.*, 1973). The most prevalent helminth overall (meta-prevalence of 73.9%) reported in tundra wolves was the nematode *Toxascaris leonina* which is a non-migratory ascarid of canids and felids whose life-cycle is essentially direct but can and often involves rodents as intermediate hosts in which third stage larval development may occur (Dunn, 1969). The high prevalence of this gut nematode likely indicates heavy predation of wolves on microtine rodents such as the tundra vole (*Microtus oeconomus*) (Rausch & Williamson, 1959).

Relatively few trematode species were recorded in wolves by comparison to cestodes and nematodes, but the strigeoid genus *Alaria* was well represented, especially in North America, though overall prevalence was no more than 5%. An individual prevalence of 62% was however recorded for wolves for one study in northern Wisconsin, USA (Archer *et al.*, 1986). These small flukes of canids and felids require three intermediate hosts to complete their life-cycle, usually snails, amphibians and rodents (Byman *et al.*, 1977), and this probably explains their apparent absence from tundra wolf populations. The occurrence of *A. canis* in 3.7% of wolves sampled in an Alaskan study probably reflects the sampling site at the boundary of boreal and tundra zones (Rausch & Williamson, 1959). Rare records of the lung fluke *Paragonimus* spp. in Palaearctic wolves indicates some predation on crustaceans, while a record of the pseudophyllidean tapeworm *Diphyllobothrium* in a wolf would indicate presence of fish in the diet (Mech, 1970). The rare but potentially pathogenic giant kidney roundworm *Dioctophyma renale* was found in five wolves in south-west Quebec, infection being obtained through ingestion of annelid worms, possibly during drinking (Dunn, 1969; McNeil *et al.*, 1984).

An analysis of published data on wolf helminths was also undertaken to compare the degree of helminth biodiversity between Nearctic and Palaearctic wolf populations and between tundra, boreal and mixed montane biomes. The Shannon-Wiener Index was applied to helminth diversity based on species number and relative prevalence, and was found to be significantly higher in wolf populations in lower latitudes of mixed montane temperate forests compared to boreal and tundra biomes. This pattern was also noted within North America by Choquette *et al.* (1973) and Marquard-Peterson (1997). However, Guberti *et al.* (1993) calculated helminth diversity to be greater in wolves from boreal forests compared to montane biomes of Italy. These latter authors nevertheless showed that parasite species assemblage ('bicenosis') was not depauperate in Italy in comparison to the larger and less disturbed populations of North American wolves, and that wolf populations in general appeared to retain characteristically structured parasite communities throughout their range. The current helminth diversity calculation using a meta-analysis of 25 studies tends to support this latter view by Guberti *et al.* (1993) as our analysis indicates that although helminth species assemblage was generally conserved, the greatest diversity of helminth species occurred in wolf populations in the temperate/montane biome within the Palaearctic region. This observation is of importance for additional consideration of preservation of helminth biodiversity in wolf populations in western Europe, in particular, because in that region their numbers are threatened by reduced habitat and indiscriminant hunting.

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