

THE RED FOX - *TRICHINELLA* RELATIONSHIP: A REVIEW OF PAST AND RECENT EVIDENCE

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ABSTRACT - In central and southern Europe, the red fox *Vulpes vulpes* is considered the reservoir of the parasite nematode *Trichinella britovi*, whose mainly fox-to-fox transmission would involve cannibalism in mountainous areas. Reviewing available literature, we examine the main ecological features of the host-parasite relationship, pointing out those aspects which do not agree with the currently accepted epidemiological pattern and requiring further research.

Key words: *Trichinella britovi*, *Vulpes vulpes*, diet, scavenging behaviour, epidemiology

RIASSUNTO - *Il binomio volpe –Trichinella: analisi di dati progressi e recenti riportati in letteratura.* In Europa centro-meridionale la volpe *Vulpes vulpes* è considerata il principale serbatoio del nematode parassita *Trichinella britovi*, la cui trasmissione da volpe a volpe sarebbe assicurata da fenomeni di cannibalismo ricorrenti in ambiente montano. Esaminando la letteratura disponibile, vengono evidenziati i principali aspetti ecologici legati alla relazione ospite-parassita che non si accordano con il modello epidemiologico corrente e che richiedono ulteriori ricerche per essere pienamente compresi.

Parole chiave: *Trichinella britovi*, *Vulpes vulpes*, dieta, scavenging, epidemiologia

INTRODUCTION

The parasite nematodes of the genus *Trichinella* belong to five encapsulated species (*T. spiralis*, *T. nativa*, *T. britovi*, *T. nelsoni*, *T. murrelli*), parasitising only mammals, and three non encapsulated species (*T. pseudospiralis*, *T. papuae*, *T. zimbabwensis*), which have been detected in mammals, birds and reptiles. The taxonomic status of three further genotypes, T6, T8 and T9, is still undetermined (Pozio and Zarlenga, 2005). The genus has a wide geographic distribution, the presence of

each parasitic species being mainly influenced by environmental temperature (Pozio *et al.*, 2002). In Europe four species have been recognised: *T. spiralis* (ubiquitous), *T. britovi* (temperate zones), *T. nativa* (frigid zones) and *T. pseudospiralis* (probably ubiquitous; Pozio and Zarlenga, 2005). *Trichinella* sp. is characterized by a unique life cycle, worms undergoing complete development within a single host (autohexeroxy). Infection is acquired through the ingestion of meat harbouring first-stage larvae, which in the columnar epithelium of the host

small intestine, moult four times before developing into adults. After mating, females produce live new-born larvae which spread through the entire host body through the bloodstream or lymph vessels, localizing into skeletal muscle cells as intracellular parasites. Host cells are transformed in “nurse cells”, which support the parasite’s growth and survival for many years (Despommier, 1983 and 1990). Encapsulating *Trichinella* species induce also the formation of a collagen capsule around nurse cells (Capó and Despommier, 1996; Pozio and Bruschi, 2001).

Trichinella sp. is widespread mainly among warm-blooded animals, the parasite having been detected in about 150 mammal species (Campbell, 1983 and 1988; Dick and Pozio, 2001). These numbers are almost certainly underestimated, considering that records of infection are often occasional and that there is lack of planned research for many potential host species.

Two main epidemiological cycles are considered. The domestic cycle involves mainly *T. spiralis* and domestic animals (pigs and horses) and rats, whose role in the epidemiology of the nematode has been debated since the formulation of Leuckart’s “Rattentheorie” in 1860 (Marazza, 1960; Pozio and Zarlenga, 2005). The sylvatic cycle occurs in wildlife and involves mainly scavenging carnivores, the eating of carrion being considered the principal mechanism of transmission of the nematode (Campbell, 1988). Synanthropic animals and improper human behaviour may contribute to the flow of *Trichinella* sp.

from wildlife to domestic animals and vice versa (Pozio, 2000).

Variants of the sylvatic cycle have been described in relation to the host and parasite species involved in different parts of the world (Campbell, 1988; Pozio, 2000 and 2001).

The red fox (*Vulpes vulpes*) is generally considered the main reservoir of the infection in most parts of temperate Europe, where *T. britovi* is the etiological agent of the sylvatic cycle (Pozio *et al.*, 1996; Pozio, 1998; Pozio and Zarlenga, 2005) and it is sometimes implicated as the reservoir of sylvatic trichinellosis in northern Europe (Isomursu and Oksanen, 2004).

The bent for cannibalism of this opportunistic carnivore may play an essential role in the maintenance of the nematode, which may be transmitted mainly from fox to fox by mean of carrion feeding (Rossi *et al.*, 1992; Pozio, 1991; Pozio *et al.*, 2000).

Being hunted for both sport and “pest” control, foxes provide plenty of samples for laboratory analyses compared to other carnivores whose hunting is often forbidden. As a consequence, since Stroh’s review (1936) of *Trichinella* sp. infection in German foxes in 1919-1936, the red fox has become the target species of several diagnostic surveys aimed to assess the parasite prevalence in many countries (reviews in Campbell, 1983; Pozio, 2000; Oivanen, 2005).

Whilst in the 20th century various aspects of the parasite morphology and biology have been extensively investigated (Pozio and Murrell, 2006), the modes of transmission of the infection among wild hosts have still not been adequately supported by

behavioural studies, which are often hindered by the elusive behaviour of carnivores and their ability to cope with a wide range of environmental conditions.

Even in 1960, examining foxes from most regions of northern Italy, Marazza suggested that the observed variation in *Trichinella* sp. prevalence and distribution was probably the result of several undetermined ecological factors acting simultaneously. Reviewing available literature concerning foxes and *Trichinella* sp., this paper aims to stress those ecological aspects of the host-parasite relationship which may play a main role in the epidemiology of trichinellosis and suggests future research for a more complete understanding of this parasite.

THE FOOD HABITS OF THE RED FOX

Surprisingly few studies relating carnivore diet to the epidemiological picture of trichinellosis have been carried out. In central Italy, *T. britovi* prevalence in wolves (*Canis lupus*) was compared to dietary data, finding no evidence of cannibalism or predation on foxes, which, in turn, showed lower rates of infection than wolves (Scaramozzino *et al.*, 1993).

In north-western European Russia, Casulli *et al.* (2001) attributed the high rate of infection (*T. nativa*) found in wolves to the consumption of carcasses of domestic dogs and wolves left as bait by hunters.

In the western Italian Alps, Remonti *et al.* (2005) studied fox diet in relation to *T. britovi* prevalence in wild carnivores, suggesting that necrofagy may not

be the only way of transmission of the nematode.

Using a different approach, Rossi and Balbo (1993), considering the red fox as the main *Trichinella* host, distributed fox carcasses in various habitats of north-western Italy to test the species attitude towards cannibalism.

Red fox diet has been investigated in a variety of habitats, throughout its wide distribution range. All studies underline the opportunistic feeding behaviour of the fox, which can use practically any edible food of animal as well as of vegetable origin, depending on the seasonal and local availability of the resources (e.g. Niewold, 1973; Ables, 1975; Lloyd, 1975; Macdonald, 1977; Doncaster *et al.*, 1990; Jedrzejewski and Jedrzejewska, 1992). Reports of cannibalism are rare and mostly referred to cub-eating (Frank, 1979) or improper human behaviour (foxes eating conspecific carcasses dug out when re-opening earths closed during rabies control campaign; Jensen and Sequeira, 1978), though Macdonald (1977) reported a case of active fox-on-fox predation. Nonetheless, Macdonald (1977) carried out several trials to test fox preference for different foods and his results suggesting that foxes loathe the meat of their conspecifics and, in general, that of carnivores.

It must be pointed out that many reports of fox diets provide the frequency of occurrence of gross items - such as "carrion", "other mammals" or "other vertebrates" -, which are useless for assessing the role played by cannibalism or scavenging. These approximations probably rise from the difficulty of distinguishing hairs at

species level and from the tendency to group those items whose occurrence is (seems) negligible.

From the extensive literature on the food habits of foxes, we selected available reports concerning Italy, where the fox is believed to be the main reservoir of several zoonoses (Pozio, 1984 and 1991), considering only those reporting the frequency of occurrence of large and medium size mammals in detail (N = 17). The consumption of carnivores was negligible (Tab. 1), except for a few reports, particularly that of Leinati *et al.* (1960).

Until the beginning of the 1980s, this work was the only one concerning fox diet in Italy and consequently had a great influence on the idea that foxes are cannibals. Nevertheless, the authors specified that most faeces contained only few hairs, probably resulting from coat cleaning, whilst “only in a few cases the hairs were numerous”, suggesting the real eating of a conspecific. As suggested by Remonti *et al.* (2005), the unintentional swallowing of hairs during coat cleaning can lead to some misunderstanding when fox hairs are found in a fox dropping, particularly during moult. From this point of view, considering that hairs are nearly always the only undigested remains of mammalian prey in fox faeces, the analysis of stomach contents is probably more reliable for assessing cannibalism. The only evidence of cannibalism in stomach contents (5/257) was reported by Pozio and Gradoni (1981), examining foxes from central Italy. This unusual result could be due to the outmoded habit of leaving

animal carcasses in the field as bait (Madsen, 1974) or to cub eating.

Also the consumption of other carnivores - mainly martens (*Martes* sp.) and domestic dogs and cats - appears to be extremely low. Predation cannot be excluded at least for cats and martens.

Scavenging seems to be an important trophic behaviour in mountain areas (Leinati *et al.*, 1960; Cagnacci *et al.*, 2003; Remonti *et al.*, 2005), where the carcasses on which foxes feed more intensively are those of wild ungulates. Dying of starvation or from avalanches, Alpine ungulates are available to foxes in winter (Green *et al.*, 1997), when hard climatic conditions limit most food resources.

It must be pointed out that the proportion of carrion used by foxes and other carnivores is not easy to assess. Necessarily, most studies consider vertebrates to have been scavenged only when their size is too large to have been killed by the animal which ate them (Witt, 1980). Evidence suggests that carnivores may also ingest a substantial proportion of small mammals that died from causes other than predation. In these terms, fresh carrion being energetic and “harmless” resources, all predators should be considered facultative scavengers (DeVault *et al.*, 2003).

THE INFLUENCE OF HABITAT ON *T. BRITTOVI* PREVALENCE IN THE RED FOX

The red fox is the European carnivore with the most extensive geographical distribution (Mitchell-Jones *et al.*, 1999). Thanks to its great ecological

Table 1 - Frequency of occurrence in the red fox diet of wild carnivores (F% c), foxes (F% f) and garbage (F% g) from 17 Italian studies reporting in detail the frequency of occurrence of mammalian prey.

N	Study area	m a.s.l.	stomachs	faeces	F% c	F% r	F% g	References
1	Western Italian Alps	700-2800		5280	12.8	12.8	13.4	Leinati <i>et al.</i> , 1960
2	Central Italy	0-1700	257		1.4	1.4	51.7	Pozio & Gradoni, 1981
3	Central Italy	0-1200	55		4.2	0	50.0	Pandolfi, 1983
4	North-Western Italy	“hills”	120		0	0	?	Ferro <i>et al.</i> , 1987
5	Central Italian Alps	300-1700		273	0	0	7.7	Cantini, 1991
6	North-Western Italy	“hills”	51		0	0	21.6	Prigioni, 1991
7	North-Western Italy	100-300	157		0	0	36.9	Debernardi <i>et al.</i> , 1991
8	Northern Italy	<200		223	0	0	4.9	Prigioni & Tacchi, 1991
9	Central Apennines	1000		264	1.0	0	4.0	Patalano & Lovari, 1993
10	Central Italy	0-800	320		0	0	?	Cavallini & Volpi, 1996
11	Northern Italy	0-250		107	0.9	0	1.9	Prigioni <i>et al.</i> , 1996
12	Northern Italy	<200		54	0	0	0	Prigioni <i>et al.</i> , 1999
13	Western Italian Alps	1000-2800		922	0	0	3.6	Cagnacci, <i>et al.</i> , 2003
14	Western Italian Alps	700-2000		180	8.3	1.6	3.4	Remonti <i>et al.</i> , 2005
			109		4.6	0	20.2	
16	North-Western Italy	0-25		115	0.9	0	0	Balestrieri <i>et al.</i> , 2005
17	Eastern Italian Alps	840-1550		133	0	0	30.1	Prigioni <i>et al.</i> , in press
18	Northern Italy	0-900	102		0	0	61.8	Meriggi <i>et al.</i> , 1990

plasticity, this species can be found in a wide variety of habitats, including urban areas, deserts and mountains up to 3000 m a.s.l., even if temperate, heterogeneous areas are preferred (Lloyd, 1980). In natural environments foxes do not select any particular habitat (e.g. Cavallini and Lovari, 1994 for Mediterranean coastal areas; Prigioni *et al.*, in press for the Italian Alps), whilst in more urbanized regions woods offer cover and seclusion (Weber and Meja, 1996).

Natural ecosystems play an important

role in the sylvatic cycle of *Trichinella* sp. in at least three continents (Pozio and Murrell, 2006). In Western Europe, the prevalence of the parasite is higher above 500 m a.s.l. or in natural parks than in lowlands (Rossi and Dini, 1990; Pozio *et al.*, 1996), suggesting that the integrity of habitat (Pozio, 1995) or, conversely, human activity (Pozio and Murrell, 2006) influence the maintenance and diffusion of the parasite among its wild hosts. At least in Italy, this pattern does not seem to be found all over the country, wide Alpine

areas showing rates of infection close to 0% (Marazza, 1960; Di Matteo *et al.*, 1991; Pozio *et al.*, 1996).

The lower incidence of fox trichinellosis in lowlands is ascribed to the high availability of food resources of human origin, such as meal and slaughtering remains and synanthropic animals (rats *Rattus* sp.), which would deter foxes from scavenging and cannibalism, lowering the risk of infection (Pozio *et al.*, 1996; Pozio and Murrell, 2006).

The strong bent for cannibalism of foxes in mountain areas is supported by field trials carried out in winter by Rossi and Balbo (1993). Placing fox carcasses in two mountain and one lowland areas, these authors found that fox feeding on conspecifics was negligible in the plain, whilst fox carcasses were "frequently" eaten between 1050 and 1900 m a.s.l. If the high consumption of conspecifics in the two Alpine areas is a consequence of the unusual, artificially increased availability of fox carrion (analogous to the previously cited baits-display for hunting), the opposite pattern shown by lowland foxes is not easy to interpret. Various local factors - food availability, individual specialization (Bolnick *et al.*, 2003), fox management (heavy hunting increases fox circumspection toward men) -, including abiotic parameters such as environmental temperature (DeVault *et al.*, 2004) can have influenced the response by lowland foxes, carrion use by scavengers being a complex process mediated by several extrinsic factors and by behavioural adaptations (Selva *et al.*, 2005). Moreover, Rossi and Balbo's study suffered from some

methodological flaws (e.g. verifiable fox density data were not reported, the number of foxes which visited the carcasses was not estimated and scavenger identification seems to be scarcely reliable) which make generalization a hazard.

Italian data on fox diet (Tab. 1) do not show a higher consumption of food resources of human origin in lowlands. Considering cumulative raw frequency data certainly carried out below or above 500 m a.s.l. (respectively, in Tab. 1: no. 7, 8, 11, 12, 16 and no. 1, 9, 13, 14, 15, 17), the use of garbage by foxes does not vary ($F\%_{<500m} = 10.8$, $F\%_{>500m} = 11.9$; $\chi^2 = 0.66$, $P = 0.42$, d.f. = 1). This lack of variation is probably due to both the presence of small domestic dumps in mountain villages (Cavada, 1997) and fox ranging behaviour in Alpine areas, where home ranges extend in length along the altitudinal gradient, including Alpine meadows as well as valley bottoms (Boitani *et al.*, 1984).

There is no evidence that habitats above 500 m a.s.l. suffer a lack of trophic resources such as to force foxes into eating a generally avoided food. Species richness peaks at middle elevations (Rahbek, 2005), as a result of a combination of ecological and historical factors and geometric constraints ("mid-domain effect"; Colwell and Lees, 2000). In addition, censuses taken in northern Italy confirm that fox abundance in hilly and pre-alpine areas is higher than that in lowlands (Prigioni *et al.*, 1991; Meriggi and Rosa, 1991; Prigioni *et al.*, 1996), which are often characterized by homogeneous mono-cultivated environments, which show a lower carrying

capacity for predators. On the other hand, the lower fox density in lowlands could play an important role in lowering the prevalence of fox trichinellosis.

Undoubtedly, harsh winter climate may limit many food resources above, approximately, 1500 m a.s.l., but at the same time it provides rich trophic resources such as ungulate carrion (Cagnacci *et al.*, 2003). Moreover, foxes can face hard times moving to lower hunting grounds (Boitani and Vinditti, 1988).

Looking at other European countries, the association between wild habitats and trichinellosis has not been found in The Netherlands, one of the most densely populated countries, where the prevalence of the nematode has been increasing since the early 1980s (Van der Giessen *et al.*, 2001).

T. BRITОВI PREVALENCE IN FOXES AND OTHER HOSTS

According to Dick and Pozio (2001), *T. britovi* has been determined in 17 mammal species and probably recovered in a further 18 species for which the identification of the nematode at species level is not certain, but which have been found infected inside the distribution range of *T. britovi*. According to more recent papers (EFSA, 2004; Pozio and Murrell, 2006), four of these dubious host species - *Sorex araneus*, *S. minutus*, *Martes martes* and *Genetta genetta* -, have been meanwhile confirmed, and two viverrids - *Nandina binotata* and *Viverra civetta* -, must be added (Pozio *et al.*, 2005). A national

survey in the Republic of Armenia lists five further mammals (*Apodemus sylvaticus*, *Microtus arvalis*, *M. majori*, *Hystrix leucara* and *Mus musculus*) among probable hosts (Asatrian *et al.*, 2004), whilst in Poland *T. britovi* has been probably isolated from *Crocidura suaveolens* (Nowosad and Lopaciuch, 2000). An old report of *T. spiralis* in a weasel (*Mustela nivalis*) may be referred to *T. britovi* (Lancastre *et al.*, 1973; Houin, pers. com.). The present total of 23 certain hosts and 21 probable ones is underestimated (Kapel, 2000) and will surely increase when more information is available for China and south-eastern Asia.

Reviewing available literature from Europe over the last 15 years (Tab. 2), what emerges more frankly is that the red fox is the target animal of epidemiological investigations throughout the continent, whilst other mammal samples are rare and almost always made up of few individuals. Prevalence range in the fox is wide, values varying between 0.1% and 36.4%.

Most studies do not report confidence intervals or statistical comparisons among different hosts or geographical areas, making it hard to evaluate the significance of prevalence variation.

Applying 95% confidence intervals (calculated as $1.96 \times \text{Standard Error}$, with $\text{SE}(p) = [p(100-p)/n]^{1/2}$; Martin *et al.*, 1987), prevalence from several countries widely overlap (Fig. 1). In southern Europe, western countries (France and Spain) show lower values than Italy, as does Switzerland, even though this country is predominantly

Table 2 - *T. britovi* prevalence (% = no. of positive cases/no. of examined cases x 100) in different hosts from 25 studies carried out in the last 15 years (Vv = *Vulpes vulpes*, Mm = *Meles meles*, Cl = *Canis lupus*, Np = *Nyctereutes procyonoides*, Ss = *Sus scrofa fera*, Ua = *Ursus arctos*, Ca = *C. aureus*, Ma = *Martes martes*; Mf = *M. foinea*, Mp = *Mustela putorius*, Ll = *Lynx lynx*, Rn = *Rattus norvegicus*); * = possibly *T. britovi* + *T. spiralis*; ^ = *T. britovi* + *T. nativa*; # = estimated value (not all isolates have been identified at species level); ≈: extremely rare.

Country	period	Prevalence (%)													References	
		Vv	Mm	Cl	Np	Ss	Ua	Ca	Ma	Mf	Mp	Ll	Rn			
Eastern Norway	1994-05	0.2														Davidson <i>et al.</i> , 2006
Finland	1996-98			5.5	1.5											Oivanen <i>et al.</i> , 2002a
Finland	1999-04											3.2				Isomursu and Oksanen, 2004
Estonia	-	42.9 [^]		80.5 [^]	45.4 [^]							51.5 [^]				Jarvis <i>et al.</i> , 2001
Estonia	1999-01											30.0 [^]	2/6			Valdmann <i>et al.</i> , 2004; Miller <i>et al.</i> , 2006
Denmark	1995-96	0.1														Enemark <i>et al.</i> , 2000
Byelorussia	-	18.2		16.2	14.1	0.9										Bekish and Odintsova, 1992
The Netherlands	1996-98	3.9														van der Giessen <i>et al.</i> , 1998
Poland	1995-99	4.1 [#]		50.0												Cabaj <i>et al.</i> , 2000; Cabai <i>et al.</i> , 2004
Slovakia (Tatra M.)	2005-06	19.7					1/1		1/3	2/5	1/3					Humikova <i>et al.</i> , 2007
Eastern Slovakia	2000-04	10.6														Letková <i>et al.</i> , 2006
Northern Caucasus	-	36.4			64.9		89.5	14.3								Sapunov and Andryuschchenko, 1992
Georgia	-						80.0	56.6								Bessonov, 1994
Azerbaijan	-	20.0						30.1								Bessonov, 1994
France	1985-95	0.6 [#]														Pozio <i>et al.</i> , 1996
Hungary	-	3.0					≈									Sréter <i>et al.</i> , 2003
Switzerland	1988-91	0.88														Gottstein <i>et al.</i> , 1997
Croatia	1996-04															Beck <i>et al.</i> , 2004.
Italy	1985-95	4.3	8.8	30.8								27.0				Pozio <i>et al.</i> , 1996
Central-South Italy	1987-93		18.7							2.2						Stancampiano <i>et al.</i> , 1993
Northern Italy	1989-90	7.4														Meriggi <i>et al.</i> , 1990
Central Italy	1991-93	4.4		28.0												Scaramozzino <i>et al.</i> , 1993
North-western Italy	1992-93	6.3				0.4										Rossi and Balbo, 1993
North-western Italy	2001-04	3.5	1.9							7.9						Remonti <i>et al.</i> , 2005
Spain (Extremadura)	1985-95	1.4														Pozio <i>et al.</i> , 1996
Spain	1997-99	8.9 [*]				0.05										Criado-Fornells <i>et al.</i> , 2000

mountainous. Ecological and maybe anthropogenic factors rather than different attitudes toward cannibalism are likely to draw such an epidemiological picture (Pozio and Murrell, 2006).

Apart from man and domestic animals, in Italy nine hosts have been determined (Dick and Pozio, 2001). Prevalence in wolves (*Canis lupus*) is higher than in all other hosts, whilst prevalence in foxes, martens (*Martes foina*) and badgers (*Meles meles*) does not significantly differ (Fig. 2). Moreover, prevalence in wolves (Scaramozzino *et al.*, 1993; Stancampiano *et al.*, 1993; Pozio *et al.*, 1996: $\chi^2 = 2.3$, $P = 0.32$, 2 d.f.) and foxes (Scaramozzino *et al.*, 1993; Rossi and Balbo, 1993; Pozio *et al.*, 1996; Remonti *et al.*, 2005: $\chi^2 = 1.4$, $P = 0.7$, 3 d.f.) does not vary among different studies. Although data are scarce, it seems that *T. britovi* occurs in medium-size carnivores with the same mean frequency, whilst the infection risk for wolves is higher. Two hypotheses, not mutually exclusive, can be drawn: i) wolves are social mammals and their prey are eaten by all members of the pack, thus a single source of trichinellosis has the opportunity of infecting several individuals at once; ii) being top-predators, wolves rely on a wider range of trophic sources which can transmit the parasite. This last hypothesis is supported by the high *T. nativa* prevalence reported for the lynx (*Lynx lynx*), a solitary predator, in northern Europe (53% vs. 33% in wolves; Oivanen *et al.*, 2002a).

The role of Mustelids has been almost always disregarded (Remonti *et al.*, 2005), although several studies have

stressed the presence of relatively high numbers of infected animals (Pozio *et al.*, 1996; Senutaité & Grikiénienė, 2001; Casulli *et al.*, 2002; Oivanen *et al.*, 2002a; Hurnikova *et al.*, 2007).

THE RELATIONSHIP BETWEEN FOX AGE AND *TRICHINELLA* PREVALENCE

The first evidence of the influence of age on the prevalence of *Trichinella* sp. came from the analysis of human cases (Gould, 1945, Piusinski, 1960). Successively, Zimmermann *et al.* in Iowa (1959a), Marazza in Italy (1960) and Roneus and Christensson in Sweden (1979) reported older foxes to have higher infection levels than young ones. More recently the same pattern has been stressed by Kanai *et al.* in Japan (2007) and by Prestrud *et al.* (1993) for arctic foxes (*Alopex lagopus*).

Infections have been found to be more common in older individuals also in other mammals, such as domestic dogs (Zimmermann and Schwarte, 1958, Oivanen *et al.*, 2005), lynx (Oksanen *et al.*, 1988) and polar bear *Ursus maritimus* (Rah *et al.*, 2005).

An easy inference is that the higher prevalence shown by older animals is a consequence of longer exposure, i.e. of increased opportunity for encountering the parasite in the surrounding environment.

Considering fox-to-fox transmission by means of fox carcass consumption, some remarks can be made. Most carrion is expected to belong to young animals, hard winter conditions taking a heavy toll on yearlings (Macdonald,

1987) and dispersion playing an important role in increasing mortality (Koopman *et al.*, 2000; Kamler *et al.*, 2004). Nevertheless, young fox carrion should have little influence upon the transmission of *Trichinella* sp., because of the age distribution of the infection. The age structure of fox populations could also influence the distribution of the nematode over wide geographic areas. Where intensive effort is put into fox control, the proportion of juveniles in the population increases, as a consequence of immigration (Phillips, 1970) or enhanced productivity (Macdonald, 1977). Life expectancy is lowered and so is expo-

sure to *Trichinella* sp. infection. In plain, homogeneous areas, “pest control” is more effective than in the mountains (Boitani and Vinditti, 1988) and could contribute to lowering nematode prevalence in lowlands.

In Italy, the epidemiological evolution of trichinellosis, following intensive fox hunting for rabies control in the 1980s, seems to support this hypothesis. The drastic decrease in prevalence all over the country (Pozio, 1991) could be a consequence of mean age reduction rather than of carcass delivery for reward (Di Matteo *et al.*, 1991).

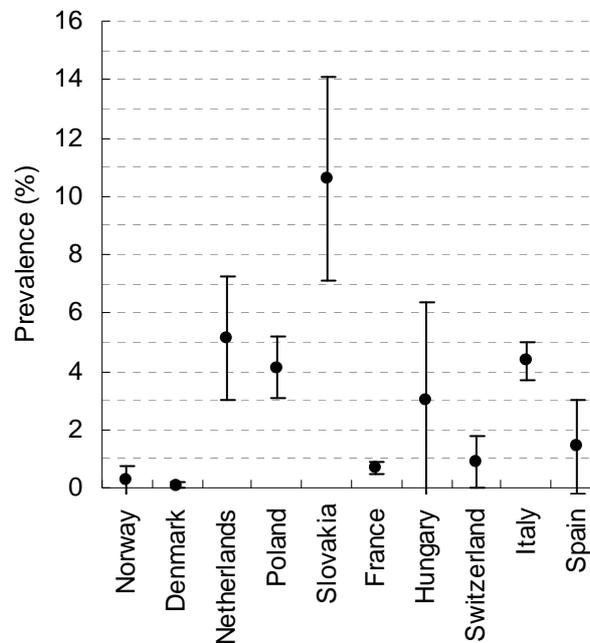


Figure 1 - Comparison of *T. britovi* prevalence in foxes (\pm 95% CI, see text) among European countries for which raw prevalence data were available.

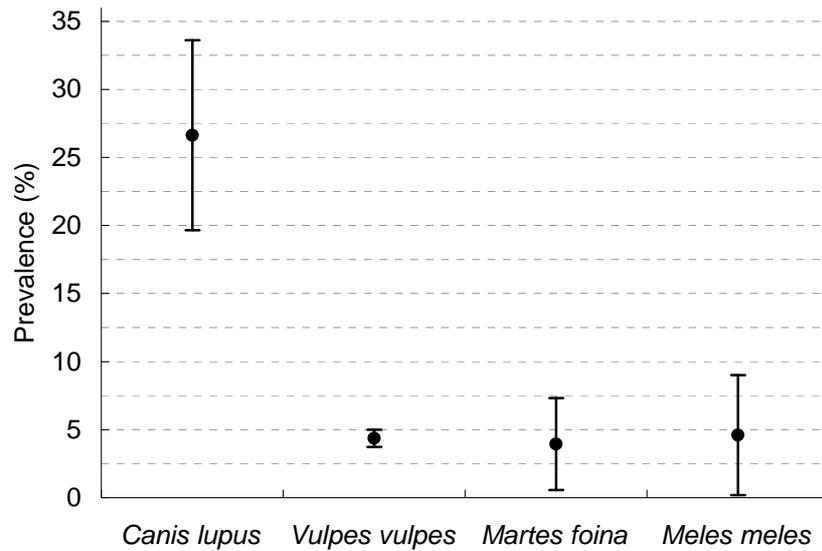


Figure 2 - Comparison of *T. britovi* prevalence (\pm 95% CI, see text) among wolves (N = 154) foxes (N = 4037), martens (N = 127) and badgers (N = 87) in Italy. Raw data from: Scaramozzino *et al.*, 1993; Stancampiano *et al.*, 1993; Rossi e Balbo, 1993; Pozio *et al.*, 1996; Remonti *et al.*, 2005.

SOME BIOLOGICAL FEATURES FAVOURING THE DISPERSAL OF *T. BRITOVII* LARVAE

Together with the lack of host specificity, the capacity of encapsulated larvae to survive after host death appears to be the most important biological feature of *Trichinella* sp., promoting interspecific transmission after host death (Campbell, 1983).

Compared to other species, *T. britovi* has a high tolerance to degradation, persisting in decaying meat for up to two weeks in fox muscles and up to four weeks in mice. Larval persistence is also influenced by the age of the infection, older larvae surviving for longer periods (von Koller *et al.*, 2001), and by environmental conditions, high humidity and low temperatures favo-

uring their survival (Bessonov, 1993). Thanks to the protection ensured by the collagen capsule, encapsulated larvae are able to remain infective even when muscle cells are completely putrefied. These “free-living” larvae are considered more resistant than many nematodes eggs or trematodes metacercariae (Madsen, 1974).

Decomposers are able to colonize carrion rapidly and produce toxins which make rotten meat inedible for scavengers (Janzen, 1977). Their activity is most effective at warm temperatures which favour bacterial and fungal growth (Putman, 1976). Scavengers must discover and eat carrion as quickly as possible, the mean time to carcass removal ranging over a few days (Simonetti *et al.*, 1984; DeVault and Rhodes, 2002; DeVault *et*

al., 2004). It appears that *T. britovi* survives in rotten meat far beyond the time necessary for scavengers to find and eat dead hosts. Longer persistence in mice seems in accord with the high percentage of small mammals probably eaten as carrion by all scavengers (Oksanen *et al.*, 1997; Smith and Merrick, 2001).

Cold temperatures inhibit decomposer activity but also represent a challenge for the survival of muscle larvae when they are no longer protected by the host homeothermy.

Trichinella species resistance to freezing reflects their geographical distribution, *T. nativa* and T6, widespread in arctic and subarctic areas of the Holarctic region, being the more tolerant species, followed by *T. britovi* (Pozio *et al.*, 1993). Also for freezing, the age of infection is correlated to resistance, full development of the nurse cell complex playing a main role in the resistance of the larvae in frozen meat. Infective *T. britovi* larvae have been found in wolf muscles after 6 months of freezing (Stancampiano *et al.*, 1993), in fox muscles after eleven months and in wild boar meat after three weeks (Dick and Pozio, 2001), whilst resistance in rodents is limited to a few days (Pozio *et al.*, 1993). In temperate climates, the opportunities for *T. britovi* to infect new hosts may be quite enhanced in winter, when mortality and climatic conditions concur to re-cycle the great biomass of the parasite concentrated in carnivores and omnivores (Campbell, 1983, Bessonov, 1993).

Besides scavenging and, eventually, predation, the transmission of the

parasite can also occur by other ways, whose role in the diffusion of *Trichinella* sp. is still not clear. Recently, the persistence of *T. spiralis* larvae from rat carcasses has been tested in four different feeds for domestic herbivores, infective larvae having been recovered after two weeks in all storage conditions (Oivanen *et al.*, 2002b). Larval persistence in pastures could explain the still untangled puzzle of infection in wild and domestic herbivores. It has been argued that *T. britovi* might be more resistant in feeds than *T. spiralis* (Oivanen, 2005).

Vertical transmission of *T. spiralis* larvae has been reported for guinea pigs, rats and rabbits and recently experimentally demonstrated in ferrets (*Mustela putorius furo*) and laboratory mice (Webster and Kapel, 2005), even if, at least for mice, the infective dose given to pregnant females seems to be much higher than any eventually acquirable in natural conditions by small mammals. Nothing is known about the transmission of *T. britovi* from pregnant females of wild species to their offspring.

Finally, *Trichinella* sp. infection can also be transmitted in faeces, even if only for short periods of time after infection, larvae surviving for a few hours once expelled (Zimmermann *et al.*, 1959b; Robinson and Olsen, 1960). The relatively long persistence of *T. britovi* larvae in the environment and the existence of a variety of secondary ways by which the nematode may propagate do not agree with a simple fox-to-fox pattern and suggest that *T. britovi* transmission could involve more than one (or a few) species,

through a variety of mechanisms which progressively end up by concentrating the parasite in top-predators.

CONCLUSIONS

In the last fifteen years, the epidemiological concept of trichinosis in central and southern Europe has been developed in the manner of a simple pattern that looks at the red fox as the main or sometimes unique reservoir of the sylvatic cycle of *T. britovi* (Macpherson, 2005; Pozio and Zarlenga, 2005; Florijancic *et al.*, 2006; Letková *et al.*, 2006; Nokler *et al.*, 2006).

Three main factors seem to have concurred to outline such a pattern: the emphasis on fox attitude toward cannibalism, its wide distribution and the disproportionate availability of fox carcasses for necropsy and analysis.

Current knowledge about fox food habits and about the distribution and age-prevalence pattern of the parasite, as also its wide range of warm-blooded hosts, suggest that fox cannibalism may not be the only way of transmission of *T. britovi* and that all carnivore species play an equal role in the nematode life-cycle.

A parasite population may establish and persist in a host population if its basic reproduction ratio, R_0 , is greater than unity (Anderson and May, 1991). R_0 is the average number of female parasites produced by each female parasite in its lifetime, in the absence of density-dependent constraints.

Considering that all the offspring of a *Trichinella* female is hosted in the muscle tissue of a single mammal (fox), the further its female larvae will

spread after host death, the higher will be its reproductive success. From this point of view, it seems essential for the parasite to infect a wide number and/or variety of hosts, the prolonged larval persistence in carrion representing a basic feature enhancing the nematode dissemination.

A transmission pattern involving a complex host community, possibly constituted by species at different levels of the trophic chain, would agree with both the wide range of known *T. britovi* hosts, which would depend on the number of species available in each geographical region, and the higher prevalence shown by top predators in natural habitats or middle elevations, where species-richness is higher.

In these terms, cannibalism would be only one - and, according to fox diet, not the most frequent -, of the mechanisms adopted by *T. britovi* to infect new hosts, relatively long-living predators being prone to accumulate weak-intensity infections spread in the biocenosis.

The hypothesis of carnivores as amplifiers of the infection is not new. In 1970, Rausch stressed the role played by the lack of host-specificity in the transmission of the parasite in the marine and sub-artic environments. Two years later, Bessonov (1972), following former soviet researchers (reviewed in Bessonov, 1993), pointed out the influence of climate on the levels of infection in both predators and small mammals. Successively, the so called carnivore-carrion transmission prevailed (Campbell, 1983), even if some authors still went against the tide (Bessonov, 1993; Stancampiano *et al.*, 1993).

The lack of sound evidence about the epidemiological role of mammals other than carnivores (rodents, insectivores and ungulates) and invertebrates (as paratenic hosts) in the sylvatic cycle of *Trichinella* sp. strongly upholds the carnivore-carrion hypothesis (Pozio and Murrell, 2006).

Considering their high densities in relation to those of predators and their importance as a trophic resource for most carnivores, small mammals (insectivores and rodents) could play a fundamental role in the epidemiology of *Trichinella* sp. and, in the past, have been considered potential hosts of the parasite by many authors (see Campbell, 1983 for a review). In the former USSR, Merkushev (1970) and Bessonov (1972) assessed levels of infection ranging from 0.03 to 0.9%. As reported above, recent isolates from micromammals are quite few and, in general, both old and recent records need verification (Pozio and Murrell, 2006). Considering that the infection in carnivores could be maintained by quite low infection rates in small mammals (Schad and Chowdhury, 1967; Pawlowski, 1978), to clear up their role is a difficult challenge (Campbell, 1983; Pozio and Murrell, 2006).

Apart from omnivorous wild boars, the few known *Trichinella* sp. infections in sylvatic ungulates represent an enigma, due to their herbivorous diet (even if horses can eat meat voluntarily; Murrell *et al.*, 2004). The recent experiment of Oivanen *et al.* (2002b) suggests that contaminated pastures could transmit the infection to herbivores. The routine analysis of game-bags in infected areas could provide more information about

the spreading of *T. britovi* in wild ungulates.

Similar studies in simulated field conditions are needed to highlight the role of carrion-eating invertebrates (Negrobov, 1960; Maroli and Pozio, 2002).

A recent mathematical model (Guberti *et al.*, 2004) suggests that the parasite should take advantage of a well structured biocenosis, supporting the carnivore-amplifiers hypothesis. The eventual successive step, from models to field evidence, will require a great effort. The correct placing of the red fox in the complex epidemiological picture of *T. britovi* could represent a good starting point for unravelling the still numerous obscure sides of its sylvatic cycle.

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