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Rodent population cycle as a determinant of gastrointestinal nematode abundance in a low-arctic population of the red fox

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ABSTRACT

We analyzed an 11-year time series (2005–2015) of parasite abundance for three intestinal nematode species in the red fox (*Vulpes vulpes*) as a function of the multi-annual rodent population cycle in low-arctic Norway, while correcting for other potential covariates that could influence prevalence and abundance. Rodents are paratenic and facultative intermediate hosts for the two Ascarididae species *Toxascaris leonina* and *Toxocara canis*, respectively and key prey for the red fox. Still the relative importance of indirect transmission through rodents and direct transmission through free-living stages is unclear. Abundance of these Ascarididae species in individual red foxes (N = 612) exhibited strongly cyclic dynamics that closely mirrored the 4-year rodent cycle. Negative binomial models provided evidence for a direct proportional increase in Ascarididae abundance with rodent density suggesting that predator functional response to rodent prey is the key transmission mechanism. In contrast, no cycles and constantly very low abundance were apparent for *Uncinaria stenocephala* – a third nematode species recorded without paratenic or intermediate stages.

1. Introduction

The gastrointestinal nematodes *Toxascaris leonina*, *Toxocara canis* and *Uncinaria stenocephala* are common parasites in the intestines of the red fox (*Vulpes vulpes*) (Saeed et al., 2006; Taylor et al., 2007; Magi et al., 2009). These three parasites can use several canine species as definitive hosts and the life cycles of *T. leonina* and *U. stenocephala* can even include feline species (Okulewicz et al. 2012). *Toxocara canis* is widespread in dogs and represent the highest zoonotic potential in urban areas (Okulewicz et al. 2012). All three nematodes are transmitted directly through oral ingestion of embryonated eggs (L2) or infective larva (L3) from the environment. The two Ascarididae species can also be transmitted through paratenic (*T. canis*) and facultative intermediate hosts (*T. leonina*) like rodents (Reperant et al., 2007; Taylor et al., 2007, Okulewicz et al. 2012). Pups can also be infected with *T. canis* via intrauterine and transmammary transmission from the vixen.

Summer temperature is an important component for development of infectious nematode stages and their survival in the environment (Gamboa, 2005; Taylor et al., 2007). In Arctic regions with short summers with low temperatures, the parasites have a relatively short transmission window. Considering that eggs need 2–6 weeks to embryonate to become infective after shedding (Okulewicz et al. 2012; Taylor et al., 2007), some parasites might not be able to become infective during one summer season. Thus, some arctic parasites have a two-year cycle for developing infectious stages (Kutz et al., 2009). This has not been described for the three fox nematodes, although for the more freeze tolerant *T. leonina,* it might be possible (Okoshi and Usui, 1968). The use of an intermediate or paratenic host can extend the transmission period beyond the short summer transmission window. Rodents infected with *T. canis* have been shown to remain infective for foxes for at least one year (Strube at al., 2013). *Toxascaris leonina* transmitted through rodents as facultative intermediate host (L2 develops into L3) reduces the prepatent period in the fox by10–15 days. The prepatent period with direct transmission is usually calculated as 10–11 weeks (Okulewicz et al. 2012; Uzal et al., 2016).

The prevalence of the three parasites in red foxes, has been shown in temperate regions, to be influenced by habitat and season (Richards et al., 1995; Gortázar et al., 1998; Saeed et al., 2006; Reperant et al., 2007). However, to what extent such variation in parasite prevalence can be attributed to specific abiotic (e.g. climate) and biotic (e.g. host density) variables is unclear, at least partly, due to lack of long-term time series data. In particular, the role of rodent hosts for the dynamics of the two Ascarididae species is not well understood (Reperant et al.,

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2007). The relative importance of transmission of the eggs from the environment and larvae from rodents is not known. Rodent populations often exhibit large fluctuations in abundance and this could influence parasite-host dynamics in several ways. Parasite transmission could increase both through predator functional response (increased consumption of infected rodents with increasing rodent abundance) and predator numerical response (i.e. increased abundance foxes shedding parasite eggs that are ingested by both hosts). Indeed, arctic rodent populations typically exhibit pronounced 3–5-year population density cycles (Ims and Fuglei, 2005; Krebs, 2013), and it is well known that red fox populations respond both numerically and functionally to these cycles (Henden et al., 2009; Killengreen et al., 2011). Climate change is, however suspected to influence the amplitude and the regularity of the rodent cycles (Ims et al., 2008; Cornulier et al., 2013) and thereby, also the epidemiology of linked parasites. Moreover, increased infection pressure and alteration in host susceptibility are also factors that may increase parasite prevalence and possible parasite disease (Taylor et al., 2007). Thus, empirical data on the dynamics of host – parasite system are vital to evaluate the impact of climate change, which presently happens at the fastest pace in the Arctic (Ims and Yoccoz, 2017).

In this study, we analyzed the dynamics of the three intestinal nematodes of the red fox (*Vulpes vulpes*) in the Varanger peninsula in the Norwegian low Arctic. Climate warming is already evident and predicted to be profound in this area in the near future (Ims et al., 2013). We combined data from an 11-year time series of parasite abundance in red foxes, rodent density and meteorological data, yielding a unique opportunity to investigate how parasite abundance in the fox population varied dependent on temporal variation in summer temperature and arctic rodent population cycles.

2. Material and methods

2.1. Study area

The study area is located in the north - eastern part of Norway on Varanger Peninsula (70–71°N). Bio-climatically, the northern and eastern part of the peninsula belong to low-arctic sub-zone E according to Walker et al. (2005), while the south-western part is classified as north boreal and partly forested (Ims et al., 2013). Relative to the latitude the climate is mild (mean temperature at the coast in January is −8.1 °C and 10.3 °C in July; data from 1961 to 1990,Norwegian Meteorological Institute, 2014). Human settlements are located only along the coast.

Red foxes are abundant and found distributed across the whole peninsula (Killengreen et al., 2012). The area also harbours a small population of an endangered population of arctic fox (*Vulpes lagopus*) (Killengreen et al., 2007; Ims et al., 2017). Dogs and domestic cats are restricted to human settlements along the coast. Three rodent species are abundant; the Norwegian lemming (*Lemmus lemmus*), the grey-sided vole (*Myodes rufocanus*) and the tundra vole (*Microtus oeconomus*) (Ims et al., 2011; Henden et al., 2011). The three rodent species exhibit a 4–5-year population cycles that are synchronous across the study area (spatial synchrony) and among the three species (inter-specific synchrony) (Ims et al., 2011, 2017; Soininen et al., 2018; Kleiven et al., 2018).

2.2. Sampling red foxes

As part of a conservation program for the endangered arctic fox population on the Varanger peninsula, an intensive campaign to cull red foxes was initiated in April 2005. During the study period (2005–2015), 2172 red foxes were culled. The foxes included in our study (N = 612) were harvested by ambush hunting by the Norwegian nature inspectorate (SNO) and by local hunters between December and April each year (Fig. 1).

The fox carcasses were kept frozen at −20 °C until necropsy and sampling took place 4–12 months later. Sex was recorded, and age was determined by cementum growth layers in the canine tooth (Jensen and Nilsen, 1968). The foxes were divided into two age classes (young ≤ 1 year old, old > 1 year old).

2.3. Monitoring rodent populations

An extensive trapping program to monitor rodent dynamics was established on Varanger peninsula in 2004. Sixty-nine trapping stations (small quadrats with 12 traps; cf. Myllymäki et al. 1971) were well dispersed on different vegetation types (Killengreen et al., 2007) and according to where red foxes were sampled on the Varanger peninsula (Fig. 1). The number of rodent individuals caught per 100 trap nights over 2 days in early September each year was used as an annual rodent density index. The 11-year study period includes two full rodent population cycles with peaks in 2007 and 2011, respectively (Fig. 2). Parasite larvae in rodents are not visible by necropsy but depends on *in vitro* digestion of muscle tissue (Takamoto et al., 1997). This diagnostic method was not performed in this study as we expected that the role of rodent population dynamics in the transmission of the parasites would be evident in terms of a statistical relation between parasite abundance in the foxes and the rodent density.

2.4. Animal care permits

Rodent trapping and sampling of red foxes were conducted as part of a combined research and conservation project that was initiated, financed and approved by The Norwegian Environmental Agency (NEA: ref no 06040003–4). NEA is the legal Norwegian authority that licenses sampling of all vertebrate wild life species for scientific purposes.

2.5. Meteorological data

Temperature and precipitation data were initially obtained from three weather stations; Vardø, Vadsø and Rustefjelmba (www.eklima.no). We used data from the summer period (mean for July, August and September) because this period was expected to be most critical for the development and transmission of the infective stages of the parasites. Due to a high correlation among the tree stations (0.82–0.92) in temperature data, only data from one station were used, Vardø (Fig. 1) to avoid strong collinearity among predictor variables. Precipitation was not correlated among the weather stations. This indicates that there is much local variation in precipitation among the sites where foxes were sampled that will not be covered by only three weather stations. Precipitation was therefore excluded as predictor variable. The mean temperature values during the study generally exceeded the 1960–90 norm (Fig. 2).

2.6. Parasitological examination

Faecal samples from the foxes were collected from the rectum or posterior colon during post-mortem examination and analysed individually for the presence of helminth eggs. A modified McMaster technique was performed with a sensitivity of 40 eggs per gram of faeces, using a saturated NaCl and glucose flotation solution (specific gravity 1,23) (Christensson et al., 1991). Egg count per gram faeces was recorded as a measure of parasite abundance of the three parasite species in individual foxes. Experimental infection of foxes shows that transmission of *T. canis* through paratenic host as well as low doses of infective eggs results in intestinal worms and thus excretion of eggs (Saeed et al., 2005). Faecal egg counts have been shown to underestimate the abundance of intestinal parasites in foxes (Saeed and Kapel, 2006; Magi et al., 2009). In this study, however, the exact egg counts were not vital as the analysis focuses on the temporal dynamics of the parasite abundance in red foxes as a function of environmental variables.

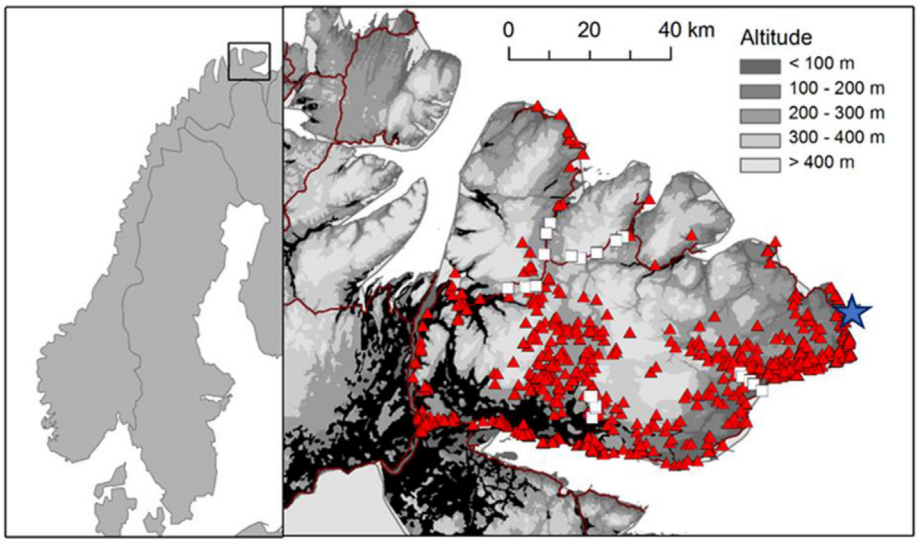

Fig. 1. Map showing the sampling sites on Varanger peninsula in northern Norway. Red triangles denote the sites where the 612 red foxes included in the analyses were. sampled. White squares denote sites where rodents were trapped for the purpose of monitoring their population dynamics. Dark areas are sub-arctic birch forest, while areas with different shading of grey show tundra at different altitudes. The meteorological station from which the climate data were derived, is denoted with a blue star. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2.7. Statistical analysis

The analyses were carried out by means of generalized linear regression models in R version 2.15.2 (R Core Team 2013) to account for the excess of zeros in the dataset. Our primary objective was to predict the prevalence and abundance of the three parasites species in the foxes as a function of the density of rodent hosts (i.e. the trapping index) and summer temperature prior to the winter when foxes were culled. In addition, number of foxes culled each winter season by local hunters was added to the model to account for temporal fluctuations in fox density (Fig. 2). Such hunting statistics is known to reflect the numerical response of red fox to rodent cycles (Henden et al., 2009). The gender and age of the foxes were also included in the models to account for annual variation in the demographic structure of the fox samples. Moreover, as foxes were culled at different distances from coast (Fig. 1) and in different months (December–April) these two variables were assessed as potential covariates in the models. First, we modelled parasite abundance by using the egg counts per gram faeces as the response variable assuming a negative binomial distribution. The model with lowest AIC_c was selected based on the dredge function in package MuMIn Version 1.42.1 in R. Due to a large proportion of zero counts (Table 1), which caused some under dispersion of the negative binomial models, we also ran the selected models based on presence (detection) or absence (non-detection) of eggs a response variable assuming a binomial distribution. These logistic regression models thus predict prevalence of the three parasites. For the logistic regressions we computed McFadden's pseudo R-squared values for the each of the predictors as $R^2 = 1\text{-}LL_{Pred}/LL_{Null}$, where LL_{Pred} and LL_{Null} is the log-likelihood for the selected model and null model, respectively.

3. Results

The average abundance and prevalence of the Ascarididae species had profound cyclic fluctuations that closely mirrored that of the rodent density cycle (Fig. 2). However, the cycle of *T. leonina* had a higher amplitude (range of annual mean egg counts: 29.3–628.4, range annual prevalence: 13.0–87.1%) than the cycle of *T. canis* (range egg counts: 7.1–94.2, range prevalence: 3.5–41.2%). In contrast to the two Ascarididae species, *U. stenocephala* had on the whole, much lower values and relatively little inter-annual variability (range egg counts: 0–43.9, range prevalence: 0–16.1%).

For *T. leonina* the model including sex, age, distance to coast, rodent abundance and the month foxes were cull best explained the variance in parasite abundance. While the model best explaining abundance of *T. canis* included sex and rodent abundance. As could be expected from the temporal prevalence dynamics (Fig. 2), rodent abundance was a highly significant predictor with very similar coefficients for both species (Tables 2 and 3), while none of the predictor variables explained the presence of *U. stenocephala*. The prevalence of the two Ascarididae species were highest in male foxes and the prevalence of *T. leonina* increased with distance to the coast and decreased during the winter months (Tables 2 and 3).

4. Discussion

The three intestinal nematodes exhibited highly contrasting multi-annual prevalence dynamics in the red fox population over the 11-year study period. The two Ascarididae species known to have rodents as paratenic or facultative intermediate host fluctuated violently in a cyclic manner that closely mirrored the rodent density cycle, while *U. stenocephala* had much less variation and showed no relationship with the rodent cycles.

That high rodent abundance may increase the prevalence of *T. leonina* in its definitive host (i.e. foxes) has previously been indirectly inferred from spatial comparisons. Stien et al. (2010) found that the prevalence of *T. leonina* in Arctic foxes decreased with distance to an area with introduced vole population in high-arctic Svalbard. Reperant et al. (2007) found that the prevalence of the same parasite in red foxes declined over a rural – urban gradient in Switzerland and assumed this to reflect a gradient in the abundance or composition of the rodent community. They stressed however, that the role of rodent intermediate hosts in the population dynamics of *T. leonina* needed to be confirmed with further studies. Moreover, Reperant et al. (2007) found no gradient in the prevalence of *T. canis,* which reinforced their conclusion that the role of rodent hosts in the two Ascarididae species was not yet fully understood.

As the first study able to link a time-series of multi-annual prevalence dynamics of intestinal nematodes in red fox to a matched time-series of rodent density dynamics, we could demonstrate that cyclic rodent population dynamics played a crucial role in epidemiology of both *T. leonina* and *T. canis*. The clear proportional increase in abundance and prevalence of both of these parasites with increasing rodent density (Fig. 3) suggests that red fox ingestion of infected rodent prey is a major transmission mechanism. Indeed, our earlier studies of diets of the red foxes from the study area (Killengreen et al., 2011; Ims et al., 2017) show that the foxes increase their consumption of rodents relative to their abundance over the different phases of the rodent cycle (i.e. done according a predator functional response). Moreover, our

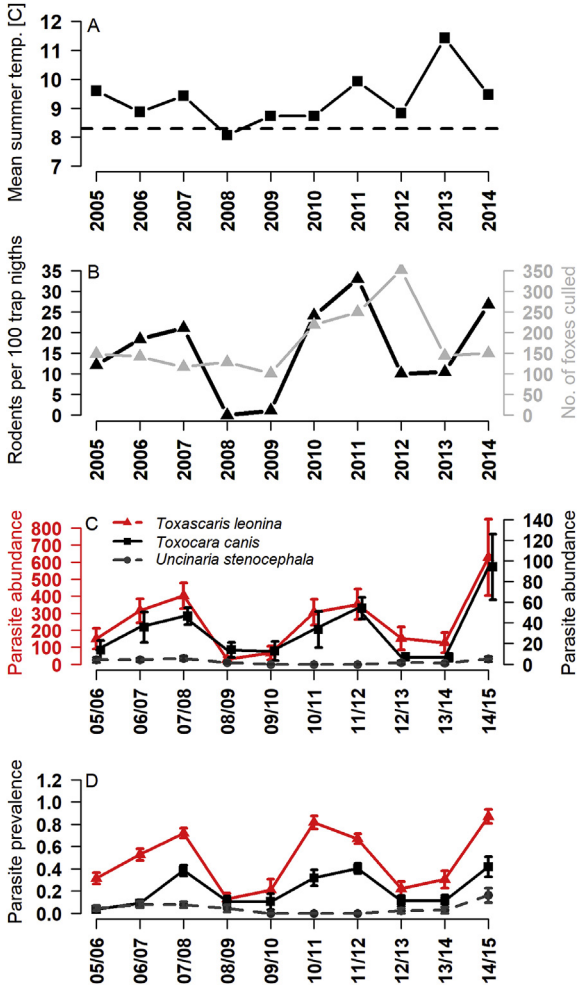

Fig. 2. Time series of annual climate variables, rodent density and egg counts of gastrointestinal parasites (i.e. number of eggs recorded) in red foxes faeces in Varanger Peninsula. A) The mean summer temperature (°C) for July, August and September from the weather station in Vardø (see Fig. 1). Horizontal broken lines show the 1960–1990 normal for temperature. B) Rodent density indexed as number of individuals caught per 100 trap nights in early September based on the trapping sites shown in Fig. 1 and number of foxes culled each winter season and local hunter (grey). Note that 2005 represents the foxes culled winter 2005–2006. C) Abundance (mean number of eggs per gram with standard error) of the three parasite species in the annual fox samples. Note the left (red) y-axis represents *T. leonina* while the right (black) y-axis represents *T. canis and U. stenocephala*. D) Prevalence (proportion of foxes with parasites, with standard error) of the three parasite species in the annual fox samples. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

finding that the prevalence of *T. leonina* increased with distance from coast is consistent with the diet studies, which showed that inland foxes have relatively more rodents in the diets than coastal foxes. Although the demography and density of boreal and arctic red fox population change over the rodent cycle (Henden et al., 2009), we do not think this

Table 2
Estimates from the best negative binomial regression models relating egg counts of (a) *Toxascaris leonina,* and (b) *Toxocara canis* in red foxes. For *T. leonina* the best model included rodent density, sex of the red fox, environmental covariate (distance from coast foxes were sampled) and the month foxes were culled, while for *T. canis* the best model included rodent density and the sex of the red fox. Significant variables are in bold. Details about model selection are given in Supplementary material.

	Estimate	Std. Error	Z-Value	P
(a) *Toxascaris leonina*				
(Intercept)	5.514	0.725		
Abundance of rodents	**0.741**	**0.119**	**6.251**	**< 0.0001**
Sex male	**0.688**	**0.239**	**2.447**	**0.004**
Distance from the coast	**0.334**	**0.123**	**2.719**	**0.007**
Month 1	0.196	0.787	0.249	0.803
Month 2	−0.303	0.745	−0.407	0.684
Month 3	−0.665	0.735	−0.905	0.366
Month 4	−1.290	0.755	−1.710	0.087
Null deviance: 619.32 on 611 d f				
Residual deviance: 574.58 on 604 d .f. Theta: 0.11917 Std. Err.: 0.00751				
(b) *Toxocara canis*				
Intercept	−2.036	0.211		
Abundance of rodents	**0.617**	**0.195**	**3.156**	**0.001**
Sex male	**1.064**	**0.396**	**2.687**	**0.007**
Null deviance: 302.30 on 611 d f				
Residual deviance: 287.17 on 609 d .f. Theta: 0.04337 Std. Err.: 0.00408				

Table 3
Estimates from logistic binomial regression models relating prevalence (i.e. detection/none-detection) of (a) *Toxascaris leonina,* and (b) *Toxocara canis* in red foxes. For *T. leonina* the best model included rodent density, sex of red fox, distance from coast where foxes were sampled and the month foxes were culled, while for *T. canis* the best model included rodent density and the sex of the red fox. R^2 are McFadden's pseudo-squared values computed as described in the main text. Significant variables are in bold.

	Estimate	Std. Error	t-Value	P
(a) *Toxascaris leonina*				
(Intercept)	0.681	0.113		
Abundance of rodents	**0.189**	**0.018**	**10.259**	**< 0.0001**
Sex male	0.070	0.037	1.883	0.060
Distance from the coast	**0.068**	**0.019**	**3.575**	**< 0.0001**
Month 1	−0.028	0.123	−0.225	0.822
Month 2	−0.175	0.116	−1.513	0.131
Month 3	**−0.233**	**0.114**	**−2.036**	**0.042**
Month 4	**−0.290**	**0.117**	**−2.466**	**0.014**
$LL_{Null=}$ −443.713 on 2 d.f.				
R^2 = 15.0 on 9 d.f.				
(b) *Toxocara canis*				
Intercept	0.153	0.0249		
Abundance of rodents	**0.116**	**0.0161**	**7.166**	**< 0.0001**
Sex male	**0.126**	**0.0327**	**3.863**	**< 0.0001**
$LL_{Null=}$ −335.982 on 2 d.f.				
R^2 = 10.15 on 4 d.f.				

Table 1
Number of red foxes with helminth eggs (left side of the slash sign) and the total number of foxes examined each winter season.

Nematodes	Hunting season (year)									
	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15
T. leonina	27/86	47/89	75/104	6/46	4/19	36/44	75/112	10/45	11/36	27/31
T. canis	3/86	8/89	40/104	5/46	2/19	14/44	45/112	5/45	4/36	13/31
U. stenocephala	4/86	7/89	8/104	2/46	0/19	0/44	0/112	1/45	1/36	5/31

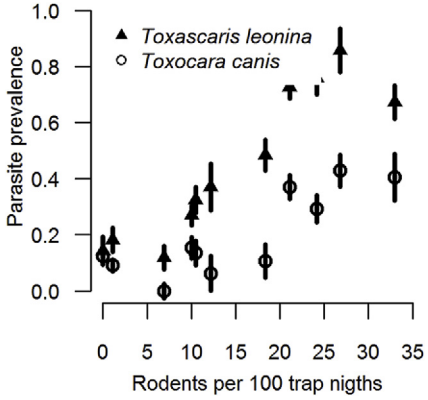

Fig. 3. Annual prevalence of the two Ascarididae species relative to rodent abundance the autumn preceding winter when the foxes were sampled.

numerical response of the predator was substantially involved in the epidemiology of the parasites. Firstly, red fox demography (age structure), which was corrected for in our statistical analyses, had no significant effects. Secondly, the number of red fox shot by local hunters each year, which is a known to be a good proxy for fox population dynamics (Henden et al., 2009), was not significant and thus not included in the best model for predicting variation in parasite abundance.

A study of the helminth *Echinococcus multilocularis* in red foxes in Japan has shown a similar strong dependence between parasite abundance in red foxes and the phases of the rodent population cycle (Saitoh and Takahashi, 1998). Other similar studies have shown that parasite transmission varies with seasonal prey preferences of the main host (Liccioli et al., 2015) or a more complex response to population cycles of different intermediate hosts (Raoul et al., 2010).

In the case of *E. multilocularis*, however, rodents are obligate intermediate hosts. It could thus be expected that high rodent densities are more essential for efficient transmission of *E. multilocularis* than for parasite species having rodents only as a facultative intermediate host (*T. leonina*) or paratenic host (*T. canis*) as transmission through free-living larval stages of the two Ascarididae species should make them less dependent on rodent hosts. Our results indicate, however, that transmission through rodent intermediate hosts is a major pathway for both *T. lenonina* and *T. canis* infections in arctic populations of the red fox.

We found no obvious effect of summer temperature on parasite abundance in the red fox. For the two Ascarididae species this could be due to the dominant impact of the rodent cycle that may have masked such an effect or that transmission of larvae through rodents buffered the impact of the abiotic environment. For *U. stenocephala* the prevalence and abundance were so low that there was practically no variation to explain.

Toxascaris leonina was more abundant than *T.canis* in our study, which is in compliance with studies from other arctic regions (Marquard-Petersen, 1997; Meijer et al., 2011; Elmore et al., 2013). *Uncinaria stenocephala* is reported as the most common nematode in red foxes in several European studies (Richards et al., 1995; Saeed et al., 2006; Reperant et al., 2007; Magi et al., 2009). The parasite is regarded as mostly monoxenous (Richards et al., 1995) and thus mainly dependent on host density and survival of free–living stages in the environment (Arneberg et al., 1998). Humidity and moist soil conditions are regarded as the major requirements for survival of eggs and larvae (Richards et al., 1995). *Uncinaria stenocephala* is reported with a relative low prevalence in arctic regions compared to temperate areas (Marquard-Petersen, 1997; Elmore et al., 2013; Smith et al., 2003; Saeed et al., 2006), indicating that the environmental conditions might be marginal in the Arctic. The prevalence in our study area was very low, but since the egg tolerance to freezing is not known the abundance might be underestimated.

5. Conclusion

By means of a uniquely long time series of the prevalence dynamics of three gastrointestinal nematode species in red foxes, rodent dynamics and meteorological data from the Norwegian low Arctic, we have been able to demonstrate that the multi-annual rodent density cycle is a key determinant of the epidemiology of the two Ascarididae species. The strong effect of rodent abundance on the abundance of *T. leonina* and *T. canis,* and the absence of any effect of red fox abundance, indicate that transmission of Ascarididae larvae hosted by rodents is presently a more important pathway for transmission than free-living larval stages. The impact of future arctic climate change on these parasites is presently uncertain. On one hand, the rodent cycles are expected to become dampened in a warmed Arctic (Ims et al., 2008; Cornulier et al., 2013), which may decrease the infections of rodent transmitted parasites in predators like the red fox. On the other hand, making predictions about climate change impacts on parasites with complex life cycles are inherently difficult (Molnár et al. 2013).

Conflicts of interest

None.

Declaration of interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijppaw.2019.03.002.

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