Intestinal parasites of the Arctic fox in relation to the abundance and distribution of intermediate hosts

A. STIEN[1]*, L. VOUTILAINEN[2], V. HAUKISALMI[2], E. FUGLEI[3], T. MØRK[4], N. G. YOCCOZ[1,5], R. A. IMS[1,5] *and* H. HENTTONEN[2]

[1] *Norwegian Institute of Nature Research* (*NINA*), *The Polar Environmental Centre*, *N-9296*, *Tromsø*, *Norway*
[2] *Vantaa Research Unit*, *Finnish Forest Research Institute*, *POB 18*, *FI-01301 Vantaa*, *Finland*
[3] *The Polar Environmental Centre*, *Norwegian Polar Institute*, *N-9296 Tromsø*, *Norway*
[4] *National Veterinary Institute*, *N-9292*, *Tromsø*, *Norway*
[5] *Department of Biology*, *University of Tromsø*, *N-9037*, *Tromsø*, *Norway*

(*Received 18 May 2009; revised 24 June 2009; accepted 25 June 2009; first published online 2 September 2009*)

SUMMARY

The intestinal parasite community of Arctic foxes (*Vulpes lagopus*) on the Svalbard archipelago in the High Arctic was investigated in relation to the abundance and distribution of intermediate hosts. Five species of cestodes (*Echinococcus multilocularis*, *Taenia crassiceps*, *Taenia polyacantha*, *Taenia krabbei* and *Diphyllobothrium* sp.), ascaridoid nematodes and one unidentified acanthocephalan species were found. The cestodes *E. multilocularis*, *T. crassiceps* and *T. polyacantha* all showed a decreasing prevalence in the fox population with increasing distance from their spatially restricted intermediate host population of sibling voles (*Microtus levis*). In addition, the prevalence of *E. multilocularis* in a sample from the vole population was directly related to the local vole abundance. The cestode *T. krabbei* uses reindeer as intermediate host, and its prevalence in female foxes was positively related to the density of reindeer (*Rangifer tarandus platyrhyncus*). Finally, the prevalence of the ascaridoid nematodes also decreased with increasing distance from the vole population, a finding that is consistent with the idea that voles are involved in transmission, most likely as paratenic hosts. The prevalence of the remaining species (*Diphyllobothrium* sp. and an unidentified acanthocephalan) was very low. We conclude that the distribution and abundance of intermediate host structure the gastrointestinal parasite community of the Arctic fox on the Svalbard archipelago.

Key words: population dynamics, density-dependent transmission, food transmission.

INTRODUCTION

A core assumption in the population dynamic theory of parasites is the existence of a positive relationship between parasite transmission rates and host population densities (e.g. Anderson and May, 1978). This relationship is expected to give rise to a curvilinear asymptotic increase in the abundance of parasites with increasing host densities (Arneberg *et al*. 1998). However, while a positive relationship between parasite abundance and host density has been found for many directly transmitted helminths (e.g. Arneberg *et al*. 1998), few studies have shown such a pattern for helminths that have intermediate hosts in their life cycle (e.g. Haukisalmi and Henttonen, 1990; Decker *et al*. 2001; Deter *et al*. 2006; Hegglin *et al*. 2007). This poor fit between theory and field observations may have a plethora of reasons, including poor estimates of the density of the available intermediate and definitive host species, and unaccounted for variability due to (1) delays in the dynamics of the parasite populations in relation to the host populations, (2) extrinsic (environmental) factors, (3) host age structure, and (4) immune responses and other density-dependent processes in the parasite population. In the High Arctic, the available number of host species is low. This makes parasite transmission networks relatively simple, and may therefore make it simpler to estimate the relationship between host densities and parasite abundances.

On the High Arctic islands of Svalbard, the Arctic fox is the terrestrial top predator and a main scavenger of carcasses. Only 2 other terrestrial mammalian species are present, the Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and the sibling vole (*Microtus levis*, earlier known as *M. rossiaemeridionalis*). The Arctic fox and the Svalbard reindeer are native species found throughout the Svalbard archipelago. In contrast, the spatial distribution of the introduced sibling vole is restricted to an 8 km stretch of coastline on the main island, Spitsbergen (Fredga *et al*. 1990; Yoccoz *et al*. 1990).

The Arctic fox on Svalbard is known to be the natural definitive host of the cestode *Taenia krabbei* which uses the reindeer as its obligatory intermediate

* Corresponding author: Norwegian Institute of Nature Research, The Polar Environmental Centre, N-9296 Tromsø, Norway. Tel: +47 77 75 04 11. Fax: +47 77 75 04 01. E-mail: audun.stien@nina.no

Parasitology (2010), **137**, 149–157.
doi:10.1017/S0031182009990953 Printed in the United Kingdom

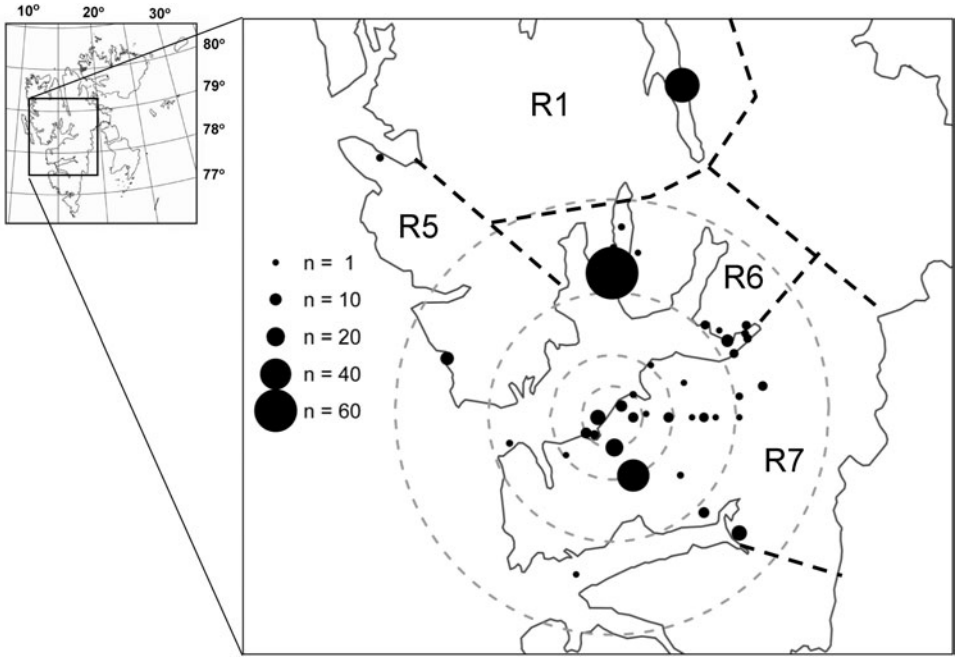

Fig. 1. The sample sites of Arctic foxes on Spitsbergen, Svalbard (black circles) with sample sizes given on a continuous scale by the size of the circles (scale given in the left part of the figure). The distances of 10, 20, 40 and 70 km from the vole population in Grumant shown as dashed grey circles. The dashed black lines give the borders between reindeer management district R1 and R5-7. The inserted map of Svalbard, with lines giving latitudinal degrees north and longitudinal degrees east, show the position of the more detailed map of the sampling area on Spitsbergen (rectangle).

host (Bye, 1985). In addition, metacestodes of *Echinococcus multilocularis* were detected in the sibling vole population on Svalbard in 1999 (Henttonen *et al*. 2001). The typical life cycle of *E. multilocularis* is sylvatic with foxes (*Vulpes vulpes*, *V. lagopus*) as definitive hosts (Rausch, 1995; Eckert and Deplazes, 2004). On Svalbard, the infection risk to Arctic foxes is restricted by the spatial extent of the sibling vole population. This causes spatial aggregation in the distribution of infected foxes and, accordingly, an *E. multilocularis* coproantigen survey found infected Arctic fox scats only in the immediate surroundings of the vole population (Fuglei *et al*. 2008).

The low biodiversity of terrestrial vertebrates on Svalbard makes their parasite communities simple with no alternative host species. Here, we analyse data on intestinal parasites of Arctic foxes (*Vulpes lagopus*) on Svalbard. We report the results from a survey of intestinal parasites of Arctic foxes, and include data from the sibling vole population on the prevalence of its vole transmitted cestodes. The focus of our analysis is on the relationship between the prevalence of the parasites and spatial patterns in the distribution and abundance of available intermediate hosts. In particular, we investigate the importance of the distance from the trap site of the foxes to the area occupied by the sibling vole population, and the reindeer density around the fox-trapping sites for parasite prevalences. In addition, patterns of infection in relation to host age and sex are reported.

MATERIALS AND METHODS

Arctic fox samples

Arctic foxes were harvested on Svalbard by fur trappers using baited traps between November 1 and March 15. A sample of 353 foxes from the 8 trapping seasons, 1996–97 ($n=10$), 1997–98 ($n=108$), 1998–99 ($n=48$), 1999–2000 ($n=32$), 2000–01 ($n=21$), 2001–02 ($n=110$), 2002–03 ($n=17$), and 2003–04 ($n=7$) was available for the present study. To remove the laboratory hazard associated with potentially *E. multilocularis* positive carcasses, the carcasses were frozen at -80 °C for a minimum of 7 days (Veit *et al*. 1995). Later storage was at -20 °C until necropsy.

The ages of 294 of the foxes were determined by counting the annuli in the cementum of a sectioned canine tooth (Grue and Jensen, 1976). Mean age was 1·8 years (S.E. = 0·12), and the oldest fox was a 13-year-old female.

For 300 of the fox samples the trappers had reported a trapping location. However, only the location of the trapping station was reported for most samples from 2 of the trapping stations and it was assumed that the foxes were trapped locally. All of the samples with a reported trapping location were from Spitsbergen, the largest island in the Svalbard archipelago (Fig. 1). The study area was divided in two by the fjord Isfjorden. The ice cover on this fjord varies substantially among and within winters depending on temperature and wind conditions. This made it difficult to devise an exact continuous

https://doi.org/10.1017/S0031182009990953 Published online by Cambridge University Press

Table 1. Number of positive samples (*n*) and prevalence with 95% CI for the different parasite species found in the 353 arctic foxes from Spitsbergen, Svalbard

	Species	*n*	Prevalence (%)	95% CI
Cestoda	*E. multilocularis*	30	8·5	6·0–11·9
	T. crassiceps	29	8·2	5·8–11·5
	T. polyacantha	51	14·4	11·1–18·5
	T. krabbei	177	50·1	45·0–55·3
	Diphyllobothrium sp.	8	2·2	1·2–4·4
Nematoda	Ascaridoid nematodes	118	33·4	28·7–38·5
Acantocephala	Acantocephalan	3	0·8	0·3–2·5

measure of shortest fox dispersal distances from the sibling vole population. To overcome this problem we grouped the samples according to distance from the vole site in the euclidean distance classes 0–10 km, 10–20 km, 20–40 km, 40–70 km, and >70 km (Fig. 1), as this grouping gives a similar order for the samples regardless whether euclidean or land – line distances were considered. In addition, the foxes were classified with respect to which reindeer management area they were trapped in. The investigated foxes were all trapped in reindeer management areas R1, R5, R6 or R7 with associated crude density estimates of 0·41, 0·46, 0·13 and 2·19 reindeer per km^2 (The Governor of Svalbard, unpublished report). The Arctic fox abundance is monitored only in a fraction of the total trapping area so that similar data on the spatial variation in the fox population density were not available.

Sibling vole samples

Sibling voles were caught in August every year using snap traps: 2001 (n=123), 2002 (n=10), 2003 (n=48), 2004 (n=46), 2005 (n=124), 2006 (n=36). The traps were placed out on the 3 sites used by Henttonen *et al.* (2001) and 1 additional site within the 8 km stretch of coastline with suitable vole habitat. In addition, a sample of voles caught in live traps in the core sibling vole site was sacrificed in September 2003 (n=87) and 2006 (n=32). The voles caught in snap traps were dissected immediately after capture, while the voles caught in live traps were euthanized and kept cool (0–5 °C) for the first 2–3 days and kept frozen thereafter until dissection. At dissection, vole sex, body weight and length to the base of the tail were recorded.

Parasitological investigations

The Arctic fox intestines were dissected at the Vantaa Research Unit of the Finnish Forest Research Institute. The small intestines were examined in 6 equally long sections and with the caecum as a seventh section. Each section was slit longitudinally, and the intestinal content and scraped mucosa were examined thoroughly under a dissecting microscope.

Voles were investigated macroscopically for metacestodes. All the livers of voles were checked for *E. multilocularis* infection and the maximum cyst diameters were measured using a ruler. During dissection of snap-trapped voles, the existence of *Taenia polyacantha* in the vole populations was confirmed twice by the finding of 1 infected vole in 2004 and 2 infected voles in 2005. However, only in the live-trapped voles were subcutaneous tissues and body cavities consistently investigated for *Taenia crassiceps* and *T. polyacantha*.

The nematodes and acanthocephalans found in the Arctic fox were transferred directly to 70% EtOH. The adult nematodes were all found to be ascaridoid nematodes. Male and juvenile nematodes could not be fully identified to species by the methods used by us, while female *Toxascaris leonina* nematodes were separated from the related *Toxocara canis* based on the shape and surface structure of their eggs. The presence of *T. leonina* was confirmed in a subsample of female nematodes investigated, while no *T. canis* were found. *T. leonina* has also been the dominant ascaridoid present in other Arctic fox populations studied (Rausch *et al.* 1983, 1990; Skirnisson *et al.* 1993; Kapel and Nansen, 1996). However, the large numbers of unidentified nematode individuals in the samples cannot exclude the possibility that *T. canis* was present also at a low prevalence.

The adult tapeworms were transferred to tap water where they were washed and relaxed for a few hours. The *Taenia* species were identified microscopically, primarily following Loos-Frank (2000), by the number, size and shape of the rostellar hooks using glycerine-ethanol (70%) preparations. It is our long-term experience that microscopic identification of these cestode species works well also on previously frozen samples. In addition to microscopic identification, the identification of *T. crassiceps* from a sibling vole and the Arctic fox, and a *T. polyacantha* from the Arctic fox, was confirmed using molecular methods (see Table 1 in Lavikainen *et al.* 2008). As *E. granulosus* is absent on Svalbard, adult *E. multilocularis* specimens were in general identified by the characteristic *Echinococcus* morphology. This

https://doi.org/10.1017/S0031182009990953 Published online by Cambridge University Press

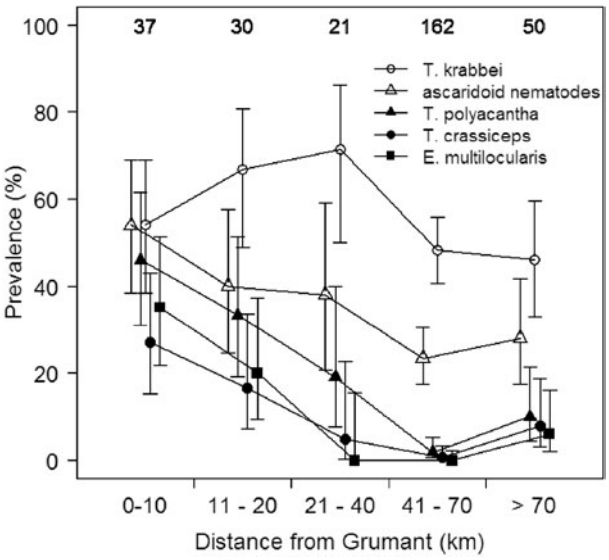

Fig. 2. Prevalence (%, ±95% CI) of the most common parasites found in the Arctic foxes with known trapping location, plotted against their distance (km) from the vole population at Grumant. Sample sizes for each distance class are given along the top row. *T. polyacantha*, *T. crassiceps* and *E. multilocularis* all use the voles as intermediate hosts, *T. krabbei* uses reindeer as intermediate host and the ascaridoid nematodes have a direct life cycle, but may also use paratenic hosts.

identification was confirmed on a sample of 12 adult *Echinococcus* specimens, collected from 3 foxes, that were stained with iron-acetocarmine and identified as *E. multilocularis* by the position of the genital pores in mature segments and the number and distribution of testes (see Rausch, 1956 and Thompson, 1995 for the identification of *Echinococcus* species). The identification of *E. multilocularis* metacestodes in the livers of voles was based on their characteristic structure with small fluid-filled pockets that contain protoscolices in mature metacestodes. This species identification was confirmed on a subsample of 10 mature metacestodes, for which the protoscolices were checked microscopically for the characteristic hook pattern. Very small metacestodes (<5 mm diameter) cannot be identified with certainty macroscopically; however, excluding these small cysts from the statistical analyses did not affect any conclusions. The identity of *E. multilocularis* metacestodes in the sibling voles on Svalbard has previously been confirmed using molecular methods (Henttonen *et al*. 2001).

Statistical analyses

Prevalence data were analysed using logistic regression. The predictor variables used when analysing the fox data were distance from the vole population fitted as a 5 level factor, reindeer density, fox sex and age, and year of sampling. In addition, we investigated whether the prevalence of the parasite species differed between foxes trapped ⩽10 km from the sea and more inland (>10 km from the sea), but found no effect of distance to the sea for any of the parasite species investigated (all P values >0·20). Fox age was investigated both as a linear term, a second order polynomial, fitted as a 4 level factor with animals grouped as juveniles, 1 year olds, 2–5 year olds and ⩾6 year olds, and investigated using a smoothing spline (Wood, 2006). The predictor variables when analysing the vole data were sample site, vole sex and length, and year of sampling. Model selection was based on the AIC criterion given by AIC = −2 Log likelihood + 2*np, where np is the number of parameters estimated in the model (e.g. Wood, 2006). As recommended by Agresti and Coull (1998), score test based confidence limits were calculated for the proportions reported in Table 1, Fig. 2 and Fig. 5. Logistic regression model parameters and predicted effects are given ±1 S.E. The goodness of fit of the logistic regression models was checked using the method of le Cessie and van Houwelingen (1991).

RESULTS

The Arctic fox

The parasite fauna found in the small intestine of the 353 Arctic foxes included the previously documented cestodes *E. multilocularis* and *T. krabbei*. In addition, the cestodes *T. crassiceps* and *T. polyacantha* were found for the first time on Svalbard. Both species use rodents as intermediate hosts, and therefore depend on sibling voles as their intermediate host on Svalbard. Three additional parasites were found: a cestode (*Diphyllobothrium* sp.), ascaridoid nematodes (probably predominantly *T. leonina*), and an unidentified acanthocephalan. Of these, *Diphyllobothrium* sp. and the acanthocephalan occurred in very few hosts (1–2% prevalence, Table 1), while the ascaridoid nematodes were common (33%, Table 1). The most prevalent parasite in the Arctic fox was *T. krabbei* (50%, Table 1). The vole-transmitted cestodes, *E. multilocularis*, *T. crassiceps* and *T. polyacantha*, occurred in 8–14% of the foxes and showed a high degree of species co-occurrence with 50% of the infected foxes (n = 61) being infected with more than one of these species.

The prevalence of the vole-transmitted cestodes was highest (27–46%) in Arctic foxes caught adjacent (0–10 km distance) to the vole population and decreased with increasing distance to the sibling vole population (Fig. 2). However, a low number of foxes (n = 8), of which 3 were infected with *E. multilocularis*, were found infected with these parasites more than 70 km from the vole site. In our dataset, all of these long-distance dispersal events occurred in the winter 1997–98. This was a winter with an exceptionally extensive ice cover on the fjords on

https://doi.org/10.1017/S0031182009990953 Published online by Cambridge University Press

Table 2. Analysis of deviance table and parameter estimates with S.E. for the logistic regression model analysing the prevalence of *T. polyacantha* in Arctic foxes

(The factor predictor variables 'distance to the vole site' and age >1 years were added sequentially for the analysis of deviance and the intercept was excluded when estimating the model parameters.)

Predictor	Deviance	D.F.	*P*	Parameter	Estimate	S.E.
Distance to vole site	55·9	4	<0·0001	Distance 0–10 km	−0·84	0·49
Age >1 years	11·5	1	0·001	Distance 11–20 km	−1·72	0·56
Residual	129·0	249		Distance 21–40 km	−2·50	0·74
				Distance 41–70 km	−5·28	0·82
				Distance >70 km	−2·83	0·60
				Age >1 years	1·56	0·49

Table 3. Analysis of deviance table and parameter estimates with S.E. for logistic regression model analysing the prevalence of *T. krabbei* in Arctic foxes. Terms were added sequentially

Predictor	Deviance	D.F.	*P*	Estimate	S.E.
Intercept				−1·47	0·35
Reindeer density	14·10	1	0·0001	0·73	0·20
Age	8·68	1	0·003	0·18	0·07
Sex (Male)	3·52	1	0·06	1·12	0·44
Reindeer density:Sex	3·35	1	0·07	−0·48	0·26
Residual	362·67	278			

the west coast of Spitsbergen and this may have facilitated the long distance dispersal events.

When the effect of distance to the vole population was controlled for using logistic regression, there was no evidence for a difference between foxes of different sex or age with respect to their prevalence of *E. multilocularis* or prevalence of *T. crassiceps* (all *P* values >0·18). The prevalence of *T. polyacantha* showed, however, evidence for an increase with age that predominantly was due to a lower prevalence in animals in their first year of life than in older foxes (Table 2). Prevalence of *T. polyacantha* increased from an estimated 30% in the youngest age class to 67% in older foxes trapped 0–10 km from the vole site (Table 2). As expected, none of the vole-transmitted cestodes showed evidence of a change in prevalence associated with reindeer density (all *P* values >0·17).

The prevalence of *T. krabbei* was not related to distance from the vole site ($P=0·41$), but increased with both host age and reindeer density (Table 3). However, the sample of male foxes from the reindeer management district with the lowest reindeer density had a high prevalence of infection, suggesting that the positive effect of reindeer density was mainly valid for female foxes (Table 3, Fig. 3).

As found for the vole-transmitted cestodes, the prevalence of the ascaridoid nematodes decreased also with increasing distance to the vole site (Table 4), while it showed no relationship to reindeer density

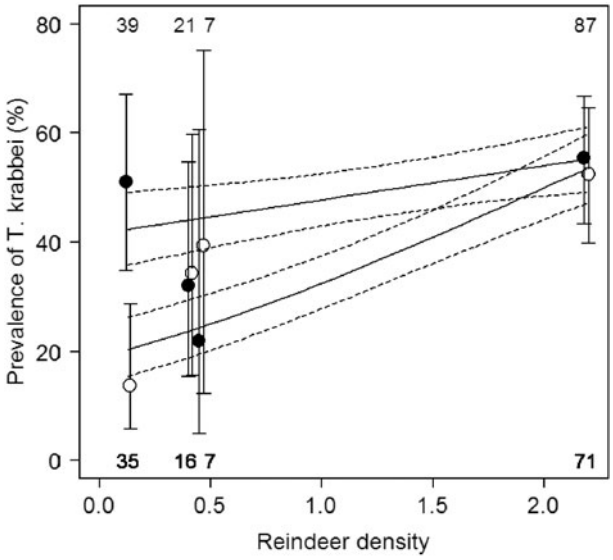

Fig. 3. Estimated (±95% CI) and predicted prevalence (%, ±1 S.E.) of *T. krabbei* in male (filled circles and top line) and female (open circles and lower line) 1-year-old Arctic foxes in relation to estimated reindeer density (km^{-2}) in the trapping area. Predictions are based on the model given in Table 2 and point estimates are based on the same model structure, but with reindeer density fitted as a factor. Samples sizes are given for male (above) and female (below) foxes.

($P=0·48$). In addition, its prevalence decreased with fox age, the best description of this relationship being a second order polynomial (Table 4, Fig. 4).

Cestode infections in the sibling vole population

In the voles caught using snap traps the overall prevalence of *E. multilocularis* infection was 19%. As found by Henttonen *et al.* (2001), the prevalence of *E. multilocularis* increased with increasing body size of the voles (Table 5), which is related to age and maturity. The smallest vole found infected was 95 mm long. This minimum size probably reflects the minimum vole age at which the parasite has been able to develop to a macroscopically detectable size. To remove some of the vole size-dependent

https://doi.org/10.1017/S0031182009990953 Published online by Cambridge University Press

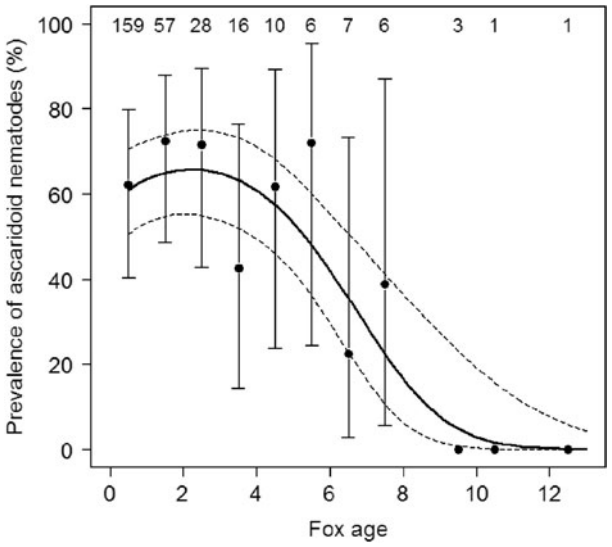

Fig. 4. Estimated (±95% CI) and predicted prevalence (%, ±1 S.E.) of ascaridoid nematodes in relation to fox age for foxes trapped 0–10 km from the vole site. Predictions are based on the model given in Table 4 and the point estimates are based on the same model structure, but with fox age fitted as a factor. Sample sizes within each age are given above the point estimates. Confidence limits have not been drawn for sample sizes <5.

variability in the prevalence of *E. multilocularis* we focused on voles of more than >100 mm length. In this subsample of voles, the prevalence showed a complex pattern with differences between sample sites, with year of sampling and vole length, and with two-way interactions between sample site and year, and sample site and vole length (Table 6). However, contrary to the findings of Henttonen *et al.* (2001), there was little evidence for a difference in *E. multilocularis* infection between male and female voles ($P=0{\cdot}22$). In one of the sites we obtained a reasonable sample of voles every year ($n=10$–81 voles per year) using 100 trap-nights each year. In this site there was a positive correlation between the prevalence of *E. multilocularis* in voles more than 100 mm long and the number of voles caught the same year, giving evidence of a density-dependent transmission rate ($r=0{\cdot}93$, $P=0{\cdot}01$, Fig. 5), and no evidence of the expected positive lagged effect of vole density on the prevalence the following year ($r=-0{\cdot}68$, $P=0{\cdot}20$).

In the sample of voles thoroughly investigated for *T. crassiceps* and *T. polyacantha*, there was an overall prevalence of *E. multilocularis* in 2003 of 10% ($n=79$) and of 16% ($n=36$) in 2006. Two voles were found with *T. crassiceps* in the 2003 sample (prevalence=2·5%) and none in 2006. No voles with *T. polyacantha* were found in these samples. Similarly, in the sample of 224 voles from 1999 and 2000 thoroughly examined by Henttonen *et al.* (2001), not a single specimen of *T. crassiceps* or *T. polyacantha* was found.

DISCUSSION

Our results show that the prevalence of the intestinal parasites of the Arctic fox on Svalbard, to a large degree, was determined by the abundance and distribution of the intermediate hosts. We found (1) a strong negative relationship between the prevalence of vole-transmitted cestodes (*E. multilocularis*, *T. crassiceps* and *T. polyacantha*) and the distance between the site the foxes were trapped and the vole population on the archipelago; (2) for female foxes a positive correlation between the prevalence of *T. krabbei*, which uses reindeer as its intermediate host, and the estimated density of reindeer in the area the foxes were trapped; (3) within the vole population, a positive relationship between the prevalence of *E. multilocularis* and the abundance of voles. In addition, the prevalence of the ascaridoid nematodes showed a negative relationship with distance to the vole population. It is likely that the nematodes were predominantly *T. leonina*, a common parasite of Arctic foxes which has basically a direct life-cycle, but has been suggested to use rodents as paratenic hosts (Rausch *et al.* 1990). The elevated prevalence near the vole population may therefore indicate that both the direct and indirect transmission routes are of importance at Svalbard, as has also been suggested for *T. leonina* in red foxes in Switzerland (Reperant *et al.* 2007).

The finding that the prevalence of the vole-transmitted parasites showed a decrease with increasing distance from the vole population was expected since a similar pattern has previously been documented by *E. multilocularis* coproantigen analyses on samples of Arctic fox faeces (Fuglei *et al.* 2008). However, while the previous survey showed a very rapid decrease in *E. multilocularis* prevalence, reaching non-detectable levels at 10 km distance from the vole site, the current study shows that infected foxes may disperse long distances during the approximately 3 months that *E. multilocularis* survive in the fox gut (Kapel *et al.* 2006). This implies that there is a risk of human *E. multilocularis* infection all over Svalbard, and, in particular, fox trappers should be aware of this hazard when handling their catch.

The long dispersal distances suggested by the parasitological data are consistent with our current understanding of the spatial ecology of the Arctic foxes on Svalbard. Reproducing Arctic foxes on Svalbard defend summer home ranges that vary in area between 4 and 60 km² (Eide *et al.* 2004). However, food availability decreases dramatically after the migrating birds have left Svalbard by October and carcasses from reindeer and seals are not available until late winter (Prestrud, 1992). Thus, Arctic foxes on Svalbard need to have an opportunistic strategy and behaviour to survive the long and dark winter, increasing the likelihood for long migrations. In particular non-breeding individuals seem to have

https://doi.org/10.1017/S0031182009990953 Published online by Cambridge University Press

Table 4. Analysis of deviance table and parameter estimates with S.E. for the logistic regression model analysing the prevalence of ascaridoid nematodes in Arctic foxes

(The predictor variables 'distance to the vole site' and terms in the second order polynomial model for 'age' were added sequentially for the analysis of deviance and the intercept was excluded when estimating the model parameters.)

Predictor	Deviance	D.F.	*P*	Parameter	Estimate	S.E.
Distance to vole site	12·29	4	0·02	Distance 0–10 km	0·44	0·43
Age	3·33	1	0·07	Distance 11–20 km	−0·56	0·42
Age^2	3·22	1	0·07	Distance 21–40 km	−0·31	0·50
Residual	297·55	249		Distance 41–70 km	−1·12	0·23
				Distance >70 km	−0·97	0·37
				Age	0·24	0·31
				Age^2	−0·068	0·043

Table 5. The prevalence of *E. multilocularis* infection in sibling voles on Svalbard given for different vole sex and length classes

(95% C I given in parentheses.)

Length class	Female	Male
66<length <90	0% (0–19)	0% (0–13)
89<length <101	3% (0–16)	5% (1–17)
100<length <111	14% (8–24)	13% (7–23)
110<length <121	28% (18–41)	42% (30–54)
120<length <131	60% (23–88)	63% (31–86)

Table 6. Analysis of deviance table for the logistic regression model analysing the prevalence of *E. multilocularis* in sibling voles longer than 100 mm length caught in snap traps

(Terms were added sequentially.)

Predictor	Deviance	D.F.	*P*
Site	39·1	3	<0·0001
Length	37·6	1	<0·0001
Year	13·0	5	0·02
Site:Year	16·5	7	0·02
Site:Length	10·4	3	0·02
Residual	194·2	253	

a migratory behaviour and may roam over areas of 500–1000 km^2 or more (Frafjord and Prestrud, 1992).

The prevalence of the vole-transmitted cestodes in the fox did not reflect their prevalence in the intermediate host. In the sibling vole population, the overall prevalence of *E. multilocularis* was 19%, while both *T. crassiceps* and *T. polyacantha* existed at prevalences close to zero. In contrast, all 3 species were found at similar prevalences in the fox population. Such a pattern has previously also been reported by Rausch *et al.* (1990) on St Lawrence Island. The difference between the parasite species in prevalence of infection in the 2 host species may be due to differences between the species in demographic rates, transmission rates and their sensitivity to host immune responses. We suggest that the pattern could be caused by very high vole consumption by the foxes when voles are available, resulting in a high probability of acquiring all 3 cestode species even at low infection levels in the voles. The finding that 50% of the foxes infected by one of the vole-transmitted cestodes were also infected by one of the other two species, is consistent with this hypothesis. The prevalence of *T. polyacantha* was slightly elevated in the fox population, when compared to the prevalence of *E. multilocularis* and *T. crassiceps*. This is probably due to the higher life expectancy of *T. polyacantha* in the fox (>2 years, Rausch and Fay, 1988) when compared to *E. multilocularis* (3 months, Kapel *et al.* 2006) and *T. crassiceps* (9 months,

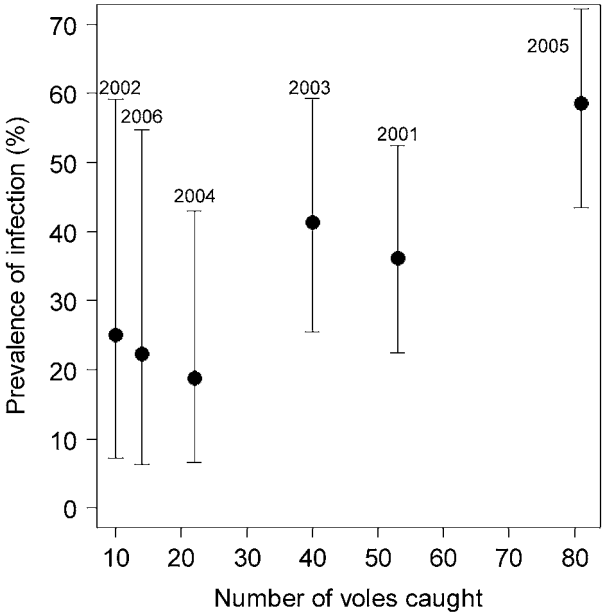

Fig. 5. Prevalence of *Echinococcus multilocularis* (±95% CI) in sibling voles with body length >100 mm, in relation to the number of voles caught at the site the same year. The year of sampling is given above the estimate.

Freeman, 1962). When voles are unavailable as prey due to e.g. fox dispersal away from the vole site, extensive snow cover or vole population crashes

https://doi.org/10.1017/S0031182009990953 Published online by Cambridge University Press

(Yoccoz and Ims, 1999), *T. polyacantha* infections will then remain for longer in the foxes than the other two species. Also the increase in *T. polyacantha* prevalence with fox age supports the notion of a high life expectancy in the fox.

Several studies have previously shown that the prevalence or abundance of *E. multilocularis* decrease with the age of its definitive host (Rausch *et al*. 1990; Torgerson, 2006), a pattern that may indicate that the host responds to infection with efficient acquired immunity (Anderson and Gordon, 1982; Woolhouse, 1993). We found no evidence for such a decrease in the prevalence of the cestode species with host age. However, indicative of such a process being important for the ascaridoid nematodes we found a marked decrease in their prevalence with host age, a pattern also previously reported for *T. leonina* in Arctic foxes (Rausch *et al*. 1990; Kapel and Nansen, 1996).

The intestinal parasite community of Arctic foxes on Svalbard was dominated by cestodes that use the sibling vole (*E. multilocularis*, *T. polyacantha* and *T. crassiceps*) or reindeer (*T. krabbei*) as their intermediate hosts. In addition, ascaridoid nematodes with a direct life cycle, which probably also use voles as paratenic hosts, were common. The other parasite species detected use fish or invertebrates as their intermediate hosts and were rare (*Diphyllobothrium* sp. and an acanthocephalan). As expected from the high arctic location and high degree of isolation, the observed parasite species richness of the Arctic fox population on Svalbard was low when compared to populations investigated in other parts of its distribution range such as Alaska, Iceland and Greenland (Rausch *et al*. 1983, 1990; Skirnisson *et al*. 1993; Kapel and Nansen, 1996). However, the identity and prevalence of the core parasites was well within the range observed in other locations where reindeer and/or rodent intermediate hosts are present.

ACKNOWLEDGEMENTS

We would like to thank the trappers for providing the arctic fox carcasses and especially the local resident trapper Harald A. Solheim who, in addition, provided help with some of the demographic data. Thanks also to the Governor of Svalbard for help with the collection of carcasses from the most remote trapping stations. We thank the Norklima research programme of the Norwegian Research Council, the Norwegian Polar Institute and the Strategic Fund of the Polar Environmental Centre for funding.

REFERENCES

Agresti, A. and Coull, B. A. (1998). Approximate is better than ''Exact'' for interval estimation of binomial proportions. *The American Statistician* **52**, 119–126.

Anderson, R. M. and Gordon, D. M. (1982). Processes influencing the distribution of parasite numbers within host populations with special emphasis on parasite-induced host mortalities. *Parasitology* **85**, 373–398.

Anderson, R. M. and May, R. M. (1978). Regulation and stability of host-parasite population interactions. I. Regulatory processes. *Journal of Animal Ecology* **47**, 219–247.

Arneberg, P., Skorping, A., Grenfell, B. T. and Read, A. F. (1998). Host densities as determinants of abundance in parasite communities. *Proceedings of the Royal Society of London, B* **265**, 1283–1289.

Bye, K. (1985). Cestodes of reindeer (*Rangifer tarandus platyrhynchus* Vrolik) on the Arctic islands of Svalbard. *Canadian Journal of Zoology* **63**, 2885–2887.

Decker, K. H. D., Duszynski, W. and Patrick, M. J. (2001). Biotic and abiotic effects on endoparasites infecting *Dipodomys* and *Perognathus* species. *Journal of Parasitology* **87**, 300–307.

Deter, J., Berthier, K., Chaval, Y., Cosson, J. F., Morand, S. and Charbonnel, N. (2006). Influence of geographical scale on the detection of density dependence in the host-parasite system, *Arvicola terrestris* and *Taenia taeniaeformis*. *Parasitology* **132**, 595–605.

Eckert, J. and Deplazes, P. (2004). Biological, epidemiological and clinical aspects of echinococcosis, a zoonosis of increasing concern. *Clinical Microbiology Reviews* **17**, 107–135.

Eide, N. E., Jepsen, J. U. and Prestrud, P. (2004). Spatial organization of reproductive Arctic foxes *Alopex lagopus*: responses to changes in spatial and temporal availability of prey. *Journal of Animal Ecology* **73**, 1056–1068.

Frafjord, K. and Prestrud, P. (1992). Home range and movements of arctic foxes *Alopex lagopus* in Svalbard. *Polar Biology* **12**, 519–526.

Fredga, K., Jaarola, M., Ims, R. A., Steen, H. and Yoccoz, N. G. (1990). The 'common vole' in Spitsbergen identified as *Microtus epiroticus* by chromosome analysis. *Polar Research* **8**, 283–290.

Freeman, R. S. (1962). Studies on the biology of *Taenia crassiceps* (Zeder, 1800) Rudolphi, 1810 (Cestoda). *Canadian Journal of Zoology* **40**, 969–990.

Fuglei, E., Stien, A., Yoccoz, N. G., Ims, R. A., Eide, N. E., Prestrud, P., Deplazes, P. and Oksanen, A. (2008). Spatial distribution of *Echinococcus multilocularis*, Svalbard, Norway. *Emerging Infectious Diseases* **14**, 73–75.

Grue, H. and Jensen, B. (1976). Annual cementum structures in canine teeth in arctic foxes (*Alopex lagopus* L.) from Greenland and Denmark. *Danish Review of Game Biology* **10**, 1–12.

Haukisalmi, V. and Henttonen, H. (1990). The impact of climatic factors and host density on the long-term population dynamics of vole helminths. *Oecologia* **83**, 309–315.

Hegglin, D., Bontadina, F., Contesse, P., Gloor, S. and Deplazes, P. (2007). Plasticity of predation behaviour as a putative driving force for parasite life-cycle dynamics: the case of urban foxes and *Echinococcus multilocularis* tapeworm. *Functional Ecology* **21**, 552–560.

Henttonen, H., Fuglei, E., Gower, C., Haukisalmi, V., Ims, R. A., Niemimaa, J. and Yoccoz, N. G. (2001). *Echinococcus multilocularis* on Svalbard: introduction of

an intermediate host has enabled the local life cycle. *Parasitology* **123**, 547–552.

Kapel, C. M. O. and Nansen, P. (1996). Gastrointestinal helminths of arctic foxes (*Alopex lagopus*) from different bioclimatological regions in Greenland. *Journal of Parasitology* **82**, 17–24.

Kapel, C. M. O., Torgerson, P. R., Thompson, R. C. A. and Deplazes, P. (2006). Reproductive potential of *Echinococcus multilocularis* in experimentally infected foxes, dogs, raccoon dogs and cats. *International Journal for Parasitology* **36**, 79–86.

Lavikainen, A., Haukisalmi, V., Lehtinen, M. J., Henttonen, H., Oksanen, A. and Meri, S. (2008). A phylogeny of members of the family Taeniidae based on mitochondrial *cox1* and *nad1* gene data. *Parasitology* **135**, 1457–1467.

Le Cessie, S. and Van Houwelingen, J. C. (1991). A goodness of fit test for binary regression models, based on smoothing methods. *Biometrics* **47**, 1267–1282.

Loos-Frank, B. (2000). An update of Verster's (1969). 'Taxonomic revision of the genus *Taenia* Linnaeus' (Cestoda) in table format. *Systematic Parasitology* **45**, 155–183.

Prestrud, P. (1992). Denning and home-range characteristics of breeding arctic foxes in Svalbard. *Canadian Journal of Zoology* **70**, 1276–1283.

Rausch, R. L. (1956). Studies on the helminth fauna of Alaska. The occurrence of *Echinococcus multilocularis* Leuckart, 1863, on the mainland of Alaska. *American Journal of Tropical Medicine and Hygiene* **5**, 1086–1092.

Rausch, R. L. (1995). Life cycle patterns and geographic distribution of *Echinococcus* species. In *Echinococcus and Hydatid Disease* (ed. Thompson, R. C. A. and Lymberty, A. J.), pp. 89–134. CAB International, Oxon, UK.

Rausch, R. L. and Fay, F. H. (1988). Postoncospheral development and cycle of *Taenia polyacantha* Leuckart, 1856 (Cestoda: Taeniidae). Second part. *Annales de Parasitologie Humaine et Comparée* **63**, 334–348.

Rausch, R. L., Fay, F. H. and Williamson, F. S. L. (1983). Helminths of the arctic fox, *Alopex lagopus* (L.), in Greenland. *Canadian Journal of Zoology* **61**, 1847–1851.

Rausch, R. L., Fay, F. H. and Williamson, F. S. L. (1990). The ecology of *Echinococcus multilocularis* (Cestoda, Taeniidae) on St Lawrence Island, Alaska. II. – Helminth populations in the definitive host. *Annales de Parasitologie Humaine et Comparée* **65**, 131–140.

Reperant, L. A., Hegglin, D., Fischer, C., Kohler, L., Weber, J.-M. and Deplazes, P. (2007). Influence of urbanization on the epidemiology of intestinal helminths of the red fox (*Vulpes vulpes*) in Geneva, Switzerland. *Parasitology Research* **101**, 605–611.

Skirnisson, K., Eydal, M., Gunnarsson, E. and Hersteinsson, P. (1993). Parasites of the arctic fox (*Alopex lagopus*) in Iceland. *Journal of Wildlife Diseases* **29**, 440–446.

Thompson, R. C. A. (1995). Biology and systematics of *Echinococcus*. In *Echinococcus and Hydatid Disease* (ed. Thompson, R. C. A. and Lymbery, A. J.), pp. 1–50. CAB International, Oxon, UK.

Torgerson, P. R. (2006). Canid immunity to *Echinococcus* spp.: impact on transmission. *Parasite Immunology* **28**, 295–303.

Veit, P., Bilger, B., Schad, V., Schäfer, J., Frank, W. and Lucius, R. (1995). Influence of environmental factors on the infectivity of *Echinococcus multilocularis* eggs. *Parasitology* **110**, 79–86.

Wood, S. N. (2006). *Generalized Additive Models: An Introduction with* R. Taylor and Francis. CRC Press, London, UK.

Woolhouse, M. E. J. (1993). A theoretical framework for immune responses and predisposition to helminth infection. *Parasite Immunology* **15**, 583–594.

Yoccoz, N. G., Steen, H. and Ims, R. A. (1990). Østmarkmus: En ny pattedyrart for Svalbard. *Fauna* **43**, 36–42 (in Norwegian).

Yoccoz, N. G. and Ims, R. A. (1999). Demography of small mammals in cold regions: the importance of environmental variability. *Ecological Bulletins* **47**, 137–144.

https://doi.org/10.1017/S0031182009990953 Published online by Cambridge University Press