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PARASITISM IN A DECLINING POPULATION OF SNOWSHOE HARES

Inge M. Keith,[1] Lloyd B. Keith,[2] and John R. Cary[2]

ABSTRACT: Prevalence and intensity of six endoparasites were determined in 346 snowshoe hares (*Lepus americanus*) obtained at Rochester, Alberta, during December–April 1981–1982, the second winter of a cyclic population decline. The data were analyzed for (1) differences among host sex and age classes, and among months and sample sources, and (2) evidence that parasitism was of demographic significance to the hare population. Prevalence and intensity of *Obeliscoides cuniculi* were consistently highest among adult hares, but rose most sharply from February to March among juveniles. In contrast, prevalence and intensity of *Nematodirus triangularis* were highest among juveniles; prevalence reached 90–100% by January, whereas intensity continued to rise through April. Prevalence and intensity of both *Trichuris leporis* and *Protostrongylus boughtoni* were highest also among juvenile hares; neither parameter exhibited a definite trend over time. Prevalences of *Taenia pisiformis* (cysticerci) and *Eimeria* spp. were unrelated to sex, age or month; but *Taenia* intensity was highest among juveniles, and *Eimeria* intensity tended to decrease from December to April. Intensities of *Nematodirus*, *Protostrongylus* and *Eimeria* were higher in male hares than in females. Prevalence and intensity were correlated directly in *Obeliscoides*, *Nematodirus*, *Trichuris* and *Eimeria*. Hares that died during trapping and handling, or from natural predation, had greater intensities of *Obeliscoides* than did animals killed on purpose. There was no indication, however, that risk of death was increased by the other parasitic infections. Age-related immune responses to parasitism (except *Obeliscoides*) were evidenced by reduced or stabilized prevalence and/or intensity among older hares. A multiple-regression model predicted depressed body weight with increasing intensities of *Nematodirus*, *Trichuris* or *Protostrongylus*. Other body-condition and reproductive indices were unassociated with parasite intensities. Within the hare population, *Obeliscoides*, *Trichuris*, *Protostrongylus* and *Taenia* had overdispersed distributions (typical of many endoparasites) that did not differ from a negative binomial. The frequency with which each possible combination of helminth species occurred within individual hares was consistent with the assumption that such infections occurred independently. There was no compelling reason to believe parasitism was a significant factor in the overwinter decline of this population of snowshoe hares.

INTRODUCTION

The snowshoe hare (*Lepus americanus*) is a boreal forest species whose population fluctuations are cyclic, of high amplitude, and well synchronized over large geographic areas (Keith, 1963; Keith and Windberg, 1978). During 1961–1977 we studied a cyclic population of snowshoe hares near Rochester, Alberta, and concluded that declines from peak densities were initiated by winter food shortage and extended by predation. Subsequent studies in Alberta (Keith et al., 1984) and the Yukon (Boutin et al., 1986), using radio telemetry to document proximate causes of death, have indicated a greater impact of predation than previously envisioned and a strong interaction of malnutrition and predation early in the cyclic decline.

Prevalence of five helminths common to showshoe hares was routinely noted during our 1961–1977 work. Recent analyses of these data showed that prevalence of *Obeliscoides cuniculi, Taenia pisiformis,* and *Dirofilaria scapiceps* fluctuated with snowshoe hare density (Keith et al., 1985). Information on *Protostrongylus boughtoni* and *Taenia serialis* was inadequate to test this relationship. Annual changes in prevalence, though often marked, were not associated with equally pronounced changes in key reproductive

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parameters. However, there was evidence of a significant impact of *Protostrongylus* on weight gains of young hares and on mean body weights of fully grown adults and juveniles.

In fall 1981 we returned to Rochester to monitor the overwinter (December–April) decline of a showshoe hare population that had peaked the previous year. We employed the usual mark–recapture techniques on three study areas to estimate densities and rates of movement and survival (Keith et al., 1984). In addition, approximately 50 hares were trapped and necropsied monthly. To help determine proximate causes of natural deaths we maintained 40–50 radio-collared hares on five study areas throughout winter, collaring new individuals with radios from those that died.

The present paper first examines overwinter prevalence and intensity of six endoparasites by month and host sex and age. It then addresses the question of the impact of parasitism on the hare population.

MATERIALS AND METHODS

Snowshoe hare collections

Most of our parasite data came from 256 snowshoe hares live-trapped during December–April 1981–1982. Of these, 190 were classified as "trap-normals" (i.e., alive and apparently well) before being killed by us. Sixty-six others were trap-sick, dead in traps, or died with no sign of predation within 6 days of radio collaring; these hares we classified as "trap or handling deaths." Thirty-three predator kills (12 intact) and seven starvation deaths also yielded information on parasitism. Because our radios transmitted a mortality signal if no movement occurred for 4 hr, we found 89% of hare carcasses and remains with 24 hr of death. At the end of the study, in late April, we shot 50 hares to retrieve transmitters; these hares were also necropsied.

Necropsy material for parasite study

Relevant to the parasite study in our necropsy protocol were the recording of sex, reproductive status, body and organ weights and femur lengths, determination of age from eyelens weight, and measurements of liver glycogen levels and femur marrow fat (Keith and Cary, 1979; Keith et al., 1984).

Material set aside, frozen in plastic bags, and later examined for helminths consisted of all internal organs including the gastro-intestinal tract. Unfrozen fecal pellets were removed from the rectum for oocyst (*Eimeria* spp.) counts, and fixed in 10% buffered formalin to assure long-term (2 yr) preservation until analysis was performed. This fixation method was used because freezing tends to destroy oocysts, and potassium dichromate is used primarily for short-term storage.

Laboratory procedures

Obeliscoides cuniculi: All worms present on the gastric mucosal surface were scraped off, flushed with water through a series of sieves, collected on the bottom (0.425-mm mesh), and transferred to a petri dish for counting. Most of these worms were adults. Our counts are best considered indices to intensity as some individuals may have been lost earlier in the necropsy when stomach ingesta were removed.

Nematodirus triangularis: Seven consecutive 10-cm sections at the proximal end of the small intestine, and four such sections at the distal end, were initially examined for adult *Nematodirus* in a sample of 11 hares. We thereby verified our previous impression that highest densities occurred proximally—in the above sample, 59% of the worms were within the first 10-cm section, and 88% were within the first 20 cm. Worm counts for the remaining 294 hares were thus confined to the proximal 10 cm of the duodenum, and thereby indexed intensity.

The mucosa was scraped with a metal spatula and viewed microscopically between glass slides. When counting adult *Nematodirus* we occasionally noted *Trichostrongylus calcaratus,* but made no attempt to enumerate that species.

Trichuris leporis: After removing the proximal 10 cm of the small intestine to count *Nematodirus*, as described above, we opened the remaining intestinal tract longitudinally, and flushed its entire contents through sieves. The worms were trapped on a 0.6-mm mesh and counted as removed. *Trichuris* was the only helminth present, though we had anticipated finding *Passalurus* and perhaps some adult cestodes.

Protostrongylus boughtoni: All major airways of the lungs were opened; adult worms were extracted with forceps and counted. Ten representative areas of lung parenchyma, including all lung lobes, were sectioned with a scalpel. Scrapings from the cut surfaces were viewed microscopically between glass slides for eggs and larvae, numbers of which were rated on a scale of 0 to 3. The foregoing examinations of lung tissue yielded indices to intensity, and doubtless conservative estimates of prevalence (Kralka, 1983).

Taenia pisiformis (cysticerci): The cysticerci of *Taenia* were recovered from all viscera, mesenteries and associated connective tissue and counted. A few cysticerci, if present in the rectal area, might have remained unnoticed in the body cavity when the gastro-intestinal tract and other organs were removed and bagged for parasite studies.

Eimeria spp.: Fecal pellets had earlier been fixed in formalin. These we blotted dry with filter paper and weighed. From a sample of about 3 g, oocyst numbers per gram of feces were estimated using the following modification of the McMaster method. Because these oocysts did not float readily in hypertonic salt solution, tap water was used. The number of oocysts settling to the bottom of the McMaster chamber rather than floating to the top was then counted. All other steps followed the usual McMaster procedures.

Voucher specimens of the parasites

Specimens of *Obeliscoides cuniculi*, *Protostrongylus boughtoni* and *Taenia pisiformis* have been deposited in the U.S. National Parasite Collection (Beltsville, Maryland 20705, USA) and assigned Nos. 78585–78587. Specimens of *Trichuris leporis*, *Nematodirus triangularis*, and *Eimeria* spp. were similarly deposited and assigned Nos. 78966–78968, respectively.

Data analysis

We used regression analyses to evaluate dependence of parasite prevalence and intensity on month (December–April) and on host sex and age. Prevalence within categories representing each combination of month, sex and age was transformed to log odds of being parasitized, and subjected to logistic regression (Dixon et al., 1983). Intensities were log transformed to minimize the relationship between variances and means, then subjected to multiple linear regression (Draper and Smith, 1981). This approach yielded the most parsimonious set of explanatory variables for both prevalence and intensity. Month, sex and age were encoded as indicator or dummy variables, and all possible interactions among them were considered in addition to the variables themselves. Chi-square was used to test any simple one-way breakdown of prevalence, and one-way analysis of variance was used for one-way breakdowns of intensity.

We also employed multiple linear regression to explore possible impacts of parasitism on body and adrenal weights, liver glycogen levels, bone-marrow and kidney fat, and earliness of testis recrudescence and first-litter conceptions. Parasite numbers were log transformed. Analyses were performed only on that subset of data that was complete for each parasite and for the requisite hare variables (month, sex, age, body size, etc.).

The negative binomial distribution was fitted (Bliss and Fisher, 1953) to the observed distribution of each parasite population within our aggregate sample of hares; goodness of fit was tested by chi-square.

RESULTS AND DISCUSSION

The trap-normal sample

Obeliscoides cuniculi: Prevalence and intensity of *Obeliscoides* at Rochester were consistently higher ($P < 0.001$) among adult hares than juveniles during December–April 1981–1982, but did not differ between the sexes (Tables 1, 2). There was a sharp increase in both prevalence and intensity from February to March especially within the juvenile cohort. This increase was doubtless part of the conspicuous annual cycle of *Obeliscoides*, documented in earlier studies of cottontail rabbits (*Sylvilagus floridanus*) and snowshoe hares (Clancy et al., 1940; Erickson, 1944; Keith et al., 1985). Such a late-winter rise, well before new infections can occur, is caused by the renewed development of arrested L_4 larvae (Gibbs et al., 1977; Measures and Anderson, 1983).

Nematodirus triangularis: In contrast to *Obeliscoides*, prevalence of *Nematodirus* was higher ($P = 0.059$) among juveniles than adults. The major difference occurred in December when 82% of juveniles vs. 38% of adults were infected (Table 1). Intensity was greater ($P < 0.001$) among juveniles throughout the entire December–April period (Table 2).

There was no difference ($P > 0.15$) in prevalence between males and females. Intensity was, however, generally greater ($P = 0.003$) among males. In the largely December–March sample of snowshoes

TABLE 1. Monthly prevalence of six endoparasites in a trap-normal sample of snowshoe hares at Rochester, Alberta, 1981–1982.

Parasite	Hare age[a] or sex	Sample size	Prevalence (%)					P[b] for differences due to		
			Dec	Jan	Feb	Mar	Apr	Age	Sex	Month
Obeliscoides cuniculi	Adult	74	50	60	38	83	75	<0.001		<0.001
	Juvenile	116	8	6	6	30	67			
Nematodirus triangularis	Adult	74	38	90	100	94	100	0.059		<0.001
	Juvenile	111	82	100	100	93	100			
Trichuris leporis	Adult	74	13	50	19	33	25	<0.001		
	Juvenile	116	38	61	63	77	67			
Protostrongylus boughtoni	Adult	73	38	30	64	50	42	0.026		
	Juvenile	114	38	88	44	64	67			
Adults	Male	94	36	78	72	68	65		0.025	
	Female	91	36	78	43	50	50			
Eggs and larvae	Adult	73	13	0	40	28	33	<0.001		
	Juvenile	114	46	73	50	46	58			
Taenia pisiformis	Adult	75	50	20	27	44	62			
	Juvenile	116	38	48	31	23	33			
Eimeria spp.	Adult	64	100	75	88	79	71			
	Juvenile	96	100	74	86	91	73			

[a] Juveniles were <1 yr old, having been born the previous summer; adults were >1 yr old. Age was determined from eye-lens weights (Keith and Cary, 1979) or from external genitalia (Keith et al., 1968).

[b] Level of significance determined by logistic regression (Dixon et al., 1983). When P values are not shown, the probability of no effect on intensity is >0.15.

examined by Boughton (1932) in Manitoba, prevalence tended also to be highest among males (29 vs. 20%, $P = 0.10$). On the other hand, Gubanov et al. (1960) reported that intensity of *Nematodirus aspinosus* was usually greater among female arctic hares (*Lepus timidus*) in Yakutia (USSR) during late winter and spring.

Prevalence of *N. triangularis* reached 90–100% by January among our Alberta snowshoes (Table 1), whereas intensity continued to rise through April ($P < 0.001$). Prevalence increased from December to February among snowshoe hares in Minnesota, and declined sharply from April to June (Erickson, 1944). In Yakutia, prevalence of *N. aspinosus* among arctic hares jumped from 50–60% during December–January to 80–90% during February–April; and mean monthly intensity exhibited a progressive eightfold increase during this December–April period (Gubanov et al., 1960). Thus in *Nematodirus*, as in *Obeliscoides*, there occurs a conspicuous "spring rise" (Levine, 1980).

Trichuris leporis: Both prevalence and intensity of *Trichuris* among juvenile snowshoes exceeded ($P < 0.001$ and $P = 0.014$) that among adults (Tables 1, 2). There were no differences ($P > 0.15$) by sex or month.

Czaplinska et al. (1965) found no difference in prevalence of *Trichuris sylvilagi* by age or sex among European hares (*Lepus europaeus*) in Poland. Monthly prevalence rose steadily from 47% in December to 85% in April, with highest intensities in March and April. Appreciably higher intensities of *T. sylvilagi* occurred among males during March–July and females during November–December. Intensity allegedly increased with age but the data were not convincing.

Protostrongylus boughtoni: Prevalence

TABLE 2. Monthly intensity of six endoparasites in a trap-normal sample of snowshoe hares at Rochester, Alberta, 1981–1982.

Parasite	Hare age[a] or sex	Sample size	Intensity (ln n)					P^b for differences due to		
			Dec	Jan	Feb	Mar	Apr	Age	Sex	Month
Obeliscoides cuniculi	Adult	44	0.54	1.00	1.75	3.26	3.20	0.017		<0.001
	Juvenile	29	0.00	0.00	0.00	2.14	2.92			
Nematodirus triangularis	Adult	67	1.20	3.00	3.12	3.40	3.73	<0.001		<0.001
	Juvenile	107	2.63	3.57	3.83	4.11	4.17			
	Male	86	1.84	3.54	3.65	3.80	4.37		0.003	
	Female	88	2.93	3.36	3.23	3.86	3.61			
Trichuris leporis	Adult	20	0.00	1.63	0.28	1.05	1.91	0.014		
	Juvenile	74	1.91	2.01	2.00	1.84	1.98			
Protostrongylus boughtoni	Adult	38	0.00	1.06	0.62	1.00	0.60			<0.001
	Juvenile	73	1.02	1.11	0.16	0.93	0.43			
Adults	Male	63	0.52	1.02	0.54	0.83	0.37			
	Female	48	0.75	1.22	0.40	1.10	0.63			
Eggs and larvae	Male	39	0.96	0.85	0.42	0.93	0.56		0.081	
	Female	46	0.36	0.65	0.45	0.58	0.38			
Taenia pisiformis	Adult	29	0.35	0.00	0.66	1.24	1.02	0.052		
	Juvenile	41	1.93	1.54	0.72	1.53	0.51			
Eimeria spp.	Male	62	8.68	7.68	6.99	7.34	5.89		0.028	<0.001
	Female	69	7.37	6.69	6.59	7.06	5.77			

[a] Juveniles were <1 yr old, having been born the previous summer; adults were >1 yr old. Age was determined from eye-lens weights (Keith and Cary, 1979) or from external genitalia (Keith et al., 1968).

[b] When P values are not shown, the probability of no effect on intensity is >0.15. Levels of significance were determined by multiple linear regression on ln(intensity).

of adult worms, and eggs and larvae, was greatest ($P < 0.026$, $P < 0.001$) among our juvenile snowshoes (Table 1). There were no age-specific differences ($P > 0.15$) in intensity (Table 2).

Prevalence of adult *Protostrongylus* was higher ($P = 0.025$) among males than females during February–April only, whereas intensity of eggs and larvae tended to be higher ($P = 0.081$) among males throughout the December–April sampling period. There were major between-month differences ($P < 0.001$) in intensity within the total sample that showed no consistent trend (Table 2).

Using the lesions of *P. boughtoni* to index prevalence, Keith et al. (1985) found little difference between juvenile and adult snowshoes at Rochester during December–April, but did note a markedly higher rate of infection among males vs. females during April–May as prevalence rose abruptly. This difference was most pronounced in adults (>1 yr old). We could not consistently use lesions to assess prevalence because they were often masked by postmortem changes in the available material.

According to Gubanov et al. (1960), prevalence and intensity were similar in adult and juvenile arctic hares by September in Yakutia, and likely remained so thereafter. A sex-specific difference also occurred there, as at Rochester, with intensities averaging higher among males during January–April.

Taenia pisiformis (cysticerci): Prevalence of *Taenia* cysticerci was similar ($P > 0.15$) in juveniles vs. adults, males vs. females, and among months during December–April (Table 1). Overall, intensity was highest ($P = 0.052$) among juveniles, but did not differ ($P > 0.15$) by sex or month (Table 2).

Mean monthly prevalences of *Taenia* cysticerci at Rochester during 1961–1977 showed a slight upward trend from December to April, with adult snowshoes tending to have somewhat higher rates of infection than juveniles (Keith et al., 1985). Prevalence did not differ between males and females in the foregoing Alberta study, or in a New Zealand study of the European rabbit (*Oryctolagus cuniculus*) (Bull, 1964).

Eimeria spp.: We found no differences ($P > 0.15$) in prevalence of *Eimeria* overwinter 1981–1982 that could be ascribed to age, sex or month (Table 1). However, males had consistently higher ($P < 0.028$) intensities of infection (Table 2), and there were differences ($P < 0.001$) in monthly intensities and a downward trend during December–April. Similarly, among arctic hares in Vologda and Stavropol regions, USSR, prevalence of *Eimeria*, and thus likely intensity as well, declined in winter (Naumov, 1947).

Because we occasionally noted broken oocysts, our counts using formalin fixed material may slightly underestimate true prevalence. However, the fact that 100% prevalence was recorded among both adult and juvenile hares in December indicates that no positive hares were missed. Furthermore, the sex-specific differences in intensity, and the downward trend during December–April, suggested that oocyst counts using the modified McMaster method described earlier provided an index of infection.

Relationship between prevalence and intensity

Prevalence is still the mainstay of many parasitological surveys, even though intensity is potentially more useful in assessing the impact of parasitism on individuals or populations (Anderson and May, 1978; May and Anderson, 1978). Field studies of wildlife populations, in particular, often have logistic and/or time-related constraints that simply do not permit parasite counts. Theoretically, prevalence and intensity should be directly related over some range of prevalence, but prevalence cannot increase beyond 100%, whereas intensity is without such a readily fixed limit.

Keith et al. (1985) selected months in which prevalence was well below 100%, then compared year-to-year changes in prevalence with cyclic fluctuations in snowshoe hare density. They suggested that such changes in prevalence were also tracking intensity, and noted the correlation ($r = 0.824$, $P < 0.01$) between monthly prevalence and intensity of *Obeliscoides cuniculi* in Erickson's (1944) data for snowshoe hares.

Because prevalence and intensity have seldom been compared in wild populations, we examined this relationship with data from four parasites (*Obeliscoides*, *Nematodirus*, *Trichuris* and *Eimeria*) that had appreciable sex- or age-specific ranges in monthly prevalence and intensity. The correlations varied from $r = 0.66$ ($P = 0.04$) for *Eimeria* spp. to $r = 0.90$ ($P < 0.01$) for *Nematodirus*, and the slopes of the regression lines for the three nematodes were similar (Fig. 1). Low and high prevalences were consistently associated with low and high intensities. It was surprising to us, however, that the variances seem to be greatest, and thus predictability least, at intermediate rather than highest prevalences.

Parasitism in trap-normal vs. other hares

We tested the hypothesis that hares dying in traps, from handling stress, or from predation, differed parasitologically from trap-normal and shot individuals. The basic idea was that parasitism might in some way affect physiology or behavior so as to increase risk of death. When sig-

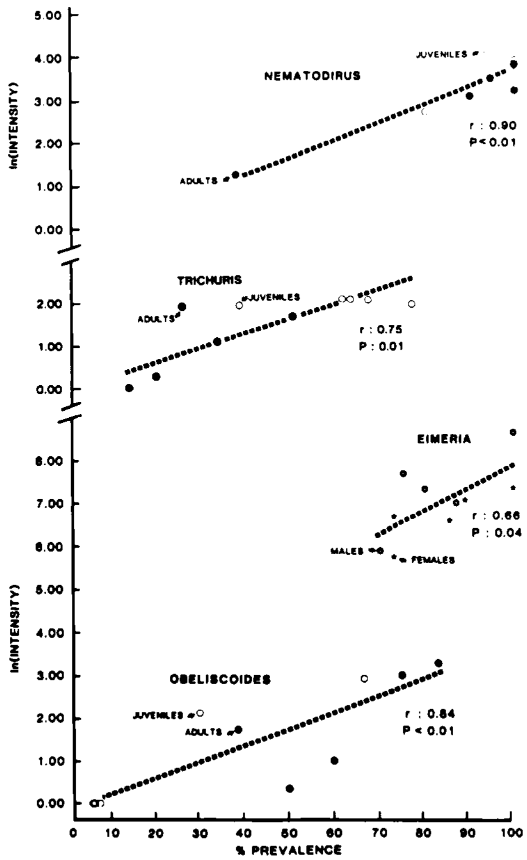


FIGURE 1. Relationship between monthly prevalence and intensity of four species of parasites in snowshoe hares from Rochester, Alberta, during December–April 1981–1982. The data were taken from Tables 1 and 2.

nificant changes in monthly prevalence or intensity occurred over the December–April period, as with *Obeliscoides*, *Nematodirus* and *Eimeria*, the data were blocked accordingly to reduce bias from time-specific differences in sampling intensity. For example, whereas trap-normal collections were distributed evenly throughout December–April, most predator kills were during late December to mid-February, and all shooting was done in late April.

In only three of nine tests did prevalence differ among the four types of samples (Table 3), and in no case was this primarily due to higher prevalence among hares dying from trapping, handling or predation. Indeed, such individuals tended to have *lower* prevalences of adult *Protostrongylus*.

During December–February, higher intensities ($P < 0.001$) of infection with *Obeliscoides* occurred among hares dying from trapping, handling and predation than among our killed trap-normals (Table 4). These months spanned a period of heavy losses to trap stress and predators that was associated with malnutrition and severe cold (Keith et al., 1984). On the other hand, intensity of *Nematodirus* was lowest in the sample of trap or handling deaths during January–April, and there was nothing suggestive of a parasite effect in the remaining data set.

Our general conclusion from this analysis is that, with the exception of *Obeliscoides*, parasitism had no detectable influence on the risk of death from stresses imposed by us through trapping and handling, nor from predation.

Parasitism in three age classes

Parasitism was shown earlier (Tables 1, 2) to vary between juvenile (5–11-mo-old) and adult hares. In summary, (1) prevalence and intensity of *Obeliscoides* were lowest among juveniles, (2) prevalence and intensity of *Nematodirus* and *Trichuris* were lowest among adults, and (3) prevalence of *Protostrongylus* and intensity of *Taenia* (cysticerci) were also lowest among adults. Such age-specific differences might reflect length of exposure, immune response, differential mortality of infected vs. noninfected individuals, or a combination of these factors. We attempted to narrow the alternatives by examining parasitism within the adult cohort—comparing prevalence and intensity among individuals that were 5–11, 17–23 and 29–35 mo old during December–April 1981–1982. No older adults were present in our sample.

TABLE 3. Prevalence (%) of parasitism among snowshoe hares from four samples sources, Rochester, Alberta, 1981–1982.

		Source of hare sample				
Parasite	Period	Killed trap-normal	Shot	Trap or handling death	Predator kill	P[a]
Obeliscoides cuniculi	Dec–Feb	23 (106)		28 (61)	37 (30)	0.291
	Mar–Apr	58 (84)	86 (50)	100 (5)	100 (3)	0.002
Nematodirus triangularis	Dec	63 (19)		33 (3)	57 (7)	0.619
	Jan–Apr	98 (166)	100 (48)	96 (56)	100 (16)	0.564
Trichuris leporis	Dec–Apr	49 (190)	48 (50)	52 (64)	67 (30)	0.347
Taenia pisiformis	Dec–Apr	37 (191)	28 (50)	32 (63)	29 (21)	0.611
Eimeria spp.	Jan–Mar	82 (117)		85 (13)		0.875
Protostrongylus boughtoni						
Adults	Dec–Apr	59 (187)	42 (48)	38 (63)	32 (19)	0.003
Eggs and larvae	Dec–Apr	45 (187)	25 (48)	48 (63)	47 (19)	0.057

[a] Levels of significance determined by chi-square.

If parasitism were a direct function of length of exposure, one would then predict increased prevalence and intensity with age. Except for a rise in prevalence of *Obeliscoides* between the 5–11- and 17–23-mo age classes (but not thereafter), this prediction was unsupported (Table 5). Prevalences and intensities of the five other parasites were stationary or declined with age, and were thus consistent with the idea that immune responses were operative. The latter appear to have been especially strong in *Trichuris* where prevalence fell steadily from 60% at age 5–11 mo to just 18% by 29–35 mo ($P < 0.001$), and in *Protostrongylus* where prevalence (of eggs and larvae) was 53% at age 5–11 mo and 26% by 29–35 mo ($P < 0.001$). Intensity of *Trichuris* likewise declined with age ($P = 0.004$), as did intensity of *Nematodirus* ($P = 0.065$).

We address the possibility of differentially higher mortality of infected individuals later in this paper.

TABLE 4. Intensity (ln n) of parasitism among snowshoe hares from four sample sources, Rochester, Alberta, 1981–1982.

		Source of hare sample					
Parasite	Period	Killed trap-normal	Shot	Trap or handling death	Predator kill	Starved	P[a]
Obeliscoides cuniculi	Dec–Feb	1.07 (24)		2.55 (17)	3.09 (11)	3.14 (1)	0.001
	Mar–Apr	2.93 (49)	3.29 (43)	2.39 (5)	4.42 (3)	1.61 (1)	0.088
Nematodirus triangularis	Dec	2.27 (12)		1.39 (1)	3.28 (4)	4.65 (1)	0.141
	Jan–Apr	3.66 (162)	3.78 (48)	3.11 (54)	3.77 (16)	3.19 (5)	0.004
Trichuris leporis	Dec–Apr	1.76 (94)	1.28 (24)	1.25 (33)	1.29 (20)	0.35 (2)	0.080
Taenia pisiformis	Dec–Apr	1.10 (70)	0.89 (14)	1.33 (20)	1.21 (6)	0.00 (1)	0.605
Eimeria spp.	Jan–Mar	7.05 (96)		7.02 (11)	6.55 (1)		0.943
Protostrongylus boughtoni							
Adults	Dec–Apr	0.78 (111)	0.62 (20)	0.57 (24)	0.44 (6)	0.17 (4)	0.236
Eggs and larvae	Dec–Apr	0.52 (85)	0.84 (12)	0.47 (30)	0.67 (9)	0.46 (3)	0.212

[a] Levels of significance determined by one-way analysis of variance.

TABLE 5. Prevalence and mean intensity of parasitism among showshoe hares in three age classes of Rochester, Alberta, December-April 1981-1982. Sample sizes are shown in parentheses.

Parasite		Approximate age of hares (months)[a]			
		5-11	17-23	29-35	P[b]
Obeliscoides cuniculi	Prevalence (%)	32 (210)	69 (78)	66 (29)	<0.001
	Intensity (ln *n*)	2.54 (67)	2.85 (54)	2.75 (19)	0.524
Nematodirus triangularis	Prevalence (%)	95 (196)	92 (75)	93 (28)	0.646
	Intensity (ln *n*)	3.63 (186)	3.46 (69)	3.11 (26)	0.065
Trichuris leporis	Prevalence (%)	60 (208)	39 (77)	18 (28)	<0.001
	Intensity (ln *n*)	1.72 (124)	0.79 (30)	1.61 (5)	0.004
Taenia pisiformis	Prevalence (%)	33 (203)	34 (77)	38 (29)	0.871
	Intensity (ln *n*)	1.17 (67)	1.06 (26)	0.71 (11)	0.327
Eimeria spp.	Prevalence (%)	80 (105)	88 (43)	77 (22)	0.411
	Intensity (ln *n*)	6.98 (84)	7.10 (38)	6.48 (17)	0.324
Protostrongylus boughtoni					
Adults	Prevalence (%)	53 (119)	47 (75)	56 (27)	0.573
	Intensity (ln *n*)	0.81 (106)	0.63 (35)	0.46 (15)	0.185
Eggs and larvae	Prevalence (%)	53 (119)	27 (75)	26 (27)	<0.001
	Intensity (ln *n*)	0.57 (105)	0.43 (20)	0.40 (7)	0.313

[a] Hares were aged by lens weights (Keith and Cary, 1979); births occur annually during May-August.

[b] Level of significance for prevalence determined by chi-square; level of significance for intensity determined by stepwise multiple linear regression on ln(intensity).

Effect of parasitism on some demographic and physiologic indices

Body weight: From earlier demographic analyses (Keith and Windberg, 1978; Keith et al., 1984) we knew that whole body weight during December-April varied with age, sex, month, sample source and body size. We suspected too that body weight would be affected by weight of stomach contents, and general body condition as reflected in marrow-fat levels. Clearly, all of the above would have to be taken into account when assessing impacts of parasites on body weight. The multiple-linear-regression analysis used by us incorporated the aforementioned variables and the intensities of each parasite.

The resulting linear model (Appendix 1) predicted that body weight was negatively related to increasing intensities of *Nematodirus* ($P < 0.001$), adult *Protostrongylus* ($P = 0.077$) and *Trichuris* ($P = 0.081$). For each unit increase in ln(1 + worm numbers), body weight declined by 23.8 g (*Nematodirus*), 15.4 g (*Protostrongylus*) and 8.7 g (*Trichuris*). Thus the predicted difference in weight between a snowshoe hare having nine *Nematodirus* in the first 10 cm of its small intestine, and another with 73 would be 48 g [23.8(ln 74 − ln 10)]; as would the predicted difference with 73 vs. 200 worms [23.8(ln 201 − ln 74)].

The foregoing associations of parasite intensity with body weight are independent of, and additive to, those between weight and the other variables shown in Table 6. The effect of each of these three parasites is likewise additive, assuming their respective intensities within individual hosts are independent of one another.

Among lagomorphs, lower body weights and reduced weight gains have been related in previous studies to nematode infections. Yuill (1964) found a significant negative association between nematode burdens and weight gains of captive cottontails, and young European rabbits from

TABLE 6. P-values for independent variables in multiple-linear-regression models that predicted seven dependent demographic and physiologic variables in a sample of snowshoe hares at Rochester, Alberta, December–April 1981–1982.[a]

	Dependent variables						
Independent variables	Body weight	Adrenal weight	Femur marrow fat	Kidney fat	Liver glycogen	Testis weight	First-litter concep. date
Body weight		0.001	<0.001			0.024	
Stomach contents wt.	0.002		<0.001	0.007			0.100
% Femur marrow fat	<0.001			<0.001	<0.001		
Femur length[b]	<0.001		0.001		0.082		0.129
Sex	0.003						
Age	<0.001					0.001	
Month	<0.001	0.004	<0.001	0.001	0.001	<0.001	
Habitat type[c]	0.075	<0.001					
Sample source[d]	<0.001	<0.001	<0.001		<0.001	<0.001	
ln n parasites							
Obeliscoides					0.003		
Nematodirus	<0.001						
Trichuris	0.081						
Protostrongylus							
Adults	0.077						
Eggs and larvae							
Taenia							
Eimeria							
R^2	0.621	0.247	0.608	0.453	0.247	0.889	0.374

[a] $P > 0.15$ not shown in table.

[b] An index to body size.

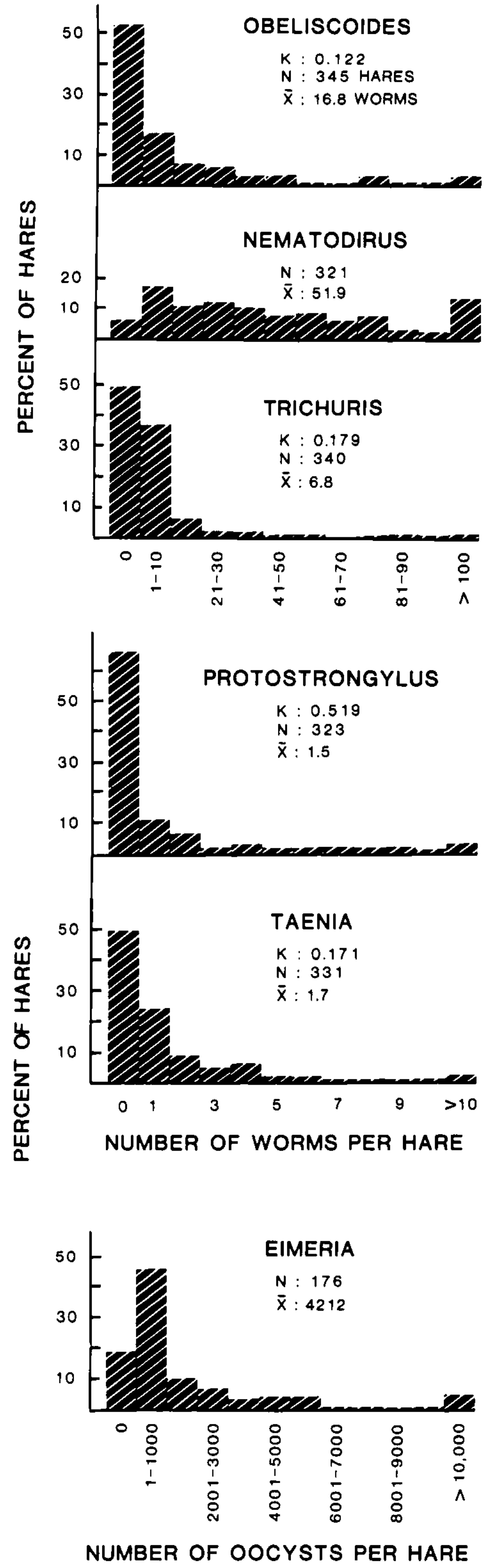
[c] Burned vs. unburned in May 1968.

[d] See Table 4.

does experimentally infected with *Trichostrongylus retortaeformis* averaged 12% lighter at weaning than young from worm-free does (Dunsmore, 1981). Bull (1964) reported an inverse relationship between numbers of *T. retortaeformis* and paunched weight of European rabbits; carcass weights of cottontail rabbits was also negatively associated with infections of *Trichostrongylus* spp. (Jacobson et al., 1978). Lighter weight of young snowshoe hares at age 37–96 days, and of fully grown adults and juveniles, were associated with *Protostrongylus boughtoni* infections (Keith et al., 1985). It is often stated that such associations may simply reflect decreased resistance of malnourished individuals to parasitism, rather than the consequence of parasitism per se. We note in this regard that worm intensities of seven snowshoes that starved to death in the wild at Rochester averaged no more than those of trap-normal individuals, even though their mean weight was 14% lighter (Keith et al., 1984).

The apparent absence of an effect of *Obeliscoides cuniculi* and *Taenia pisiformis* on body weight of snowshoe hares (Table 6) is consistent with reports from earlier rabbit and hare work (Bull, 1964; Jacobsen et al., 1978; Keith et al., 1985).

Other demographic and physiological indices: We probed for associations between intensity of parasite infection and adrenal weight, femur and kidney fat, liver glycogen, testis weight and first-litter conception date. The resulting regression models wholly excluded parasite intensity as a significant independent variable, except for a significant positive relationship



between *Obeliscoides* and liver glycogen levels (Table 6).

Evidence of parasitism affecting the above, or additional, demographic and physiologic variables in other lagomorph populations is equivocal. For example, Yuill (1964) obtained 48% more young from captive cottontails treated with anthelmintic and coccidiostatic drugs, and Bull (1964) noted lower pregnancy rates (but not fewer corpora lutea) in European rabbits with high intensities of *Trichostrongylus retortaeformis*. Dunsmore (1981) reported that worm-free European rabbit does bore about the same number of young as those experimentally infected with *T. retortaeformis*, but birth-to-weaning survival rates of these young were 96% and 82%, respectively. Keith et al. (1985) found no relationship between snowshoe hare reproductive parameters and presence or absence of *Protostrongylus boughtoni, Obeliscoides cuniculi, Dirofilaria scapiceps* or *Taenia pisiformis*. Bull (1964) similarly reported that rabbit reproduction was unaffected by *T. pisiformis, Graphidium strigosum* or *Passalurus ambigus*; and Czaplinska et al. (1965) observed that prevalence and intensity of *Trichuris sylvilagi* were significantly higher in pregnant vs. nonpregnant European hares. Naumov's (1960) comparison of embryo and *Protostrongylus* spp. counts in arctic hares disclosed no relationship.

There were negative correlations with femur fat vs. intensities of *Obeliscoides cuniculi* and *Trichostrongylus* spp., and with kidney fat vs. *Eimeria* spp., among cottontails (Jacobson et al., 1978); whereas effects of *Trichostrongylus retortaefor-*

←

FIGURE 2. Distribution of six species of parasites within the snowshoe hare population at Rochester, Alberta, during December–April 1981–1982. Values of the negative binomial parameter *k* are shown where observed distributions did not differ significantly from a negative binomial.

mis and *Graphidium strigosum* on kidney fat were either very small or nonexistent among European rabbits (Bull, 1964).

Distribution of parasites within the hare population

Parasitic helminths tend to be highly overdispersed within host populations, infections of high intensity occurring among relatively few individuals and low intensities characterizing the great majority. Negative binomial distributions with $k < 1.0$ often describe such overdispersion (Anderson and May, 1978). Four of the five helminths in our study had distributions (Fig. 2) that did not differ ($P \geq 0.12$) from appropriate negative binomials, with k ranging from 0.12 to 0.52. *Nematodirus*, however, was more uniformly dispersed throughout the hare population (Fig. 2), and the distribution of *Eimeria* also differed ($P < 0.001$) from a negative binomial.

To test the hypothesis that associations of the five helminth species within the hare population resulted from infections that occurred independently, we compared the observed frequencies of all 32 possible combinations of species with their expected frequencies assuming independent assortment (Appendix 2). The two frequency distributions did not differ ($P = 0.59$), thereby supporting the view that infections by different parasites were independent events.

Role of parasitism in the hare population decline

The snowshoe hare population at Rochester declined by 50% during December–April 1981–1982 (Keith et al., 1984). Predation was the immediate cause of 80–90% of all hare deaths, with disproportionately high losses among individuals having low femur and kidney fat, and at temperatures below −30 C.

Earlier in this paper (Tables 3, 4) prevalence and intensity of parasitism within samples of trap-normal, shot and predator-killed hares were compared. There was little indication that parasites were more prevalent or numerous among predator kills. This, to us, constitutes strong prima facie evidence that parasitism played no significant role in the population decline overwinter 1981–1982. This conclusion is further supported by the fact that intensities of parasitism were evidently no higher among hares dying from starvation (the only other natural cause of death) than among trap-normal and shot individuals.

Our failure to detect an effect of parasitism on survival of fully grown snowshoes parallels Dunsmore's (1981) assessment that neither helminths nor coccidia are a significant cause of mortality among adult rabbits in Australia.

Theoretical modelling of host–parasite interactions led Anderson and May (1978) to suggest that when density-dependent constraints on parasite population growth (typical of mammalian immune responses) are combined with overdispersion in a host population, parasite-induced mortality will not likely regulate host population growth. That conclusion may well fit our snowshoe hare population whose immune responses were evident and whose parasites were overdispersed.

We do not know if the negative relationship between parasitism and body weight, noted earlier, had any demographic significance. It seems doubtful, however, because weights of predator-killed and trap-normal hares were similar (Keith et al., 1984). The low femur and kidney fat values associated with increased risk of death from predators were evidently unrelated to parasitism (Table 6).

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APPENDIX 1. Multiple regression model predicting body weight of snowshoe hares at Rochester, Alberta, during December–April 1981–1982. Entire body weight = constant + femur marrow fat + stomach contents + weight + femur length + age + sex + habitat type + month + sample source + parasite species.

Independent variable		Variable coefficient (g)[a]	P
	Constant	1,340.82	
Discrete	Age (adult)	56.75	<0.001
	Sex (male)	−37.77	0.003
	Habitat (burned)	−24.86	0.075
	Month		
	January	32.44	0.068
	February	66.21	<0.001
	Sample source		
	Trap-normal	75.90	<0.001
	Predator-killed	127.48	<0.001
	Shot	90.96	<0.001
Continuous	Femur marrow fat	2.88	<0.001
	Stomach contents	4.07	0.002
	Femur length	191.37	<0.001
	Parasite species		
	Trichuris	−8.66	0.081
	Nematodirus	−23.82	<0.001
	Protostrongylus	−15.36	0.077

Number of cases processed: 274
$R^2 = 0.621$

[a] Coefficients for the discrete variables indicate the weight in grams added to, or subtracted from, the constant to predict body weight if the discrete variable applies. Coefficients for the continuous variables provide the weight in grams added to, or subtracted from, the constant after being multiplied by the following values: femur marrow—differences from mean fat level (%); stomach contents—difference from mean weight (g); femur length—difference from mean length (cm); *Trichuris*—ln(1 + worm numbers); *Nematodirus*—ln(1 + worm numbers); *Protostrongylus*—ln(1 + worm numbers).

APPENDIX 2. Test for independence of helminth-species infections within the snowshoe hare population at Rochester, Alberta, during December–April 1981–1982.

Possible combinations of helminths in hares (0 = absent, + = present)					Frequency distribution (number of hares)		
Obeliscoides	*Nematodirus*	*Trichuris*	*Protostrongylus*	*Taenia*	Observed	Expected[a]	Chi-square
0	+	+	+	0	32	28.09	0.54
0	+	0	+	0	29	27.04	0.14
+	+	0	0	0	27	20.94	1.75
0	+	+	0	0	26	26.69	0.02
+	+	+	0	0	23	21.76	0.07
+	+	+	+	0	20	22.89	0.37
+	+	0	+	0	20	22.03	0.19
0	+	+	+	+	19	14.52	1.38
0	+	0	0	0	18	25.69	2.30
0	+	+	0	+	13	13.80	0.05
0	+	0	+	+	12	13.97	0.28
0	+	0	0	+	12	13.28	0.12
+	+	0	+	+	12	11.39	0.03
+	+	+	0	+	12	11.25	0.05
+	+	0	0	+	12	10.82	0.13
+	+	+	+	+	9	11.83	0.68
0	0	0	0	0	5	1.56	7.56
+	0	+	+	0	2	1.39	0.27
0	0	+	+	+	2	0.88	1.41
0	0	0	0	+	2	0.81	1.76
0	0	+	+	0	1	1.71	0.29
0	0	0	+	0	1	1.64	0.25
0	0	+	0	0	1	1.62	0.24
+	0	0	+	0	1	1.34	0.09
+	0	0	0	0	1	1.27	0.06
+	0	0	+	+	1	0.69	0.14
+	0	0	0	+	1	0.66	0.18
+	0	+	0	0	0	1.32	1.32
0	0	0	+	+	0	0.85	0.85
0	0	+	0	+	0	0.84	0.84
+	0	+	+	+	0	0.72	0.72
+	0	+	0	+	0	0.68	
Totals					314	313.97	24.76 ($P = 0.59$, df = 27)

[a] The expected distribution was calculated from the observed prevalences of the five helminth species in a sample of 314 snowshoe hares for which species-prevalence information was complete. Total prevalence of each species, expressed as a proportion, was: *Obeliscoides*—0.449, *Nematodirus*—0.943, *Trichuris*—0.510, *Protostrongylus* (adults)—0.513, *Taenia*—0.341. If infection by these helminths occurs independently, then the expected probability of each of the 32 possible combinations of presence and absence is the product of species' prevalences (if present) or their complements (if absent). Thus, in the above table, the combination of 0 *Obeliscoides*, + *Nematodirus*, + *Trichuris*, 0 *Protostrongylus*, and + *Taenia* would have a probability of occurrence of $(1 - 0.449)(0.943)(0.510)(1 - 0.513)(0.341) = 0.044$. This probability multiplied by the number of hares examined (314) gives the expected tabular value of 13.8.