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Source: Journal of Wildlife Diseases, 21(3) : 233-253

Published By: Wildlife Disease Association

URL: <https://doi.org/10.7589/0090-3558-21.3.233>

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PREVALENCE OF HELMINTHS IN A CYCLIC SNOWSHOE HARE POPULATION

Lloyd B. Keith,¹ John R. Cary,¹ Thomas M. Yuill,² and Inge M. Keith³

ABSTRACT: Five species of helminths were monitored in a population of snowshoe hares (*Lepus americanus*) near Rochester, Alberta, during 1961–1977. Prevalence of both *Obeliscoides cuniculi* and *Protostrongylus boughtoni* among young hares averaged about 50% by age 2 mo, then tended to level off. Prevalence of *Taenia pisiformis* (cysticerci) and *Dirofilaria scapiceps* rose more slowly, but continued to increase steadily beyond their mean levels of 8% and 1% at age 2 mo. There were well defined seasonal (within-year) cycles in prevalence of *O. cuniculi* and *P. boughtoni* that were generated evidently to a major degree by arrested development of larvae in fall and renewed development in late winter. It was hypothesized that renewed larval development was triggered (in February) in *O. cuniculi* by the seasonal rise of circulating pituitary gonadotrophins, and (in April) in *P. boughtoni* by the seasonal rise of gonadal androgens and estrogens. Indices to gonadal hormone levels in hares indicated that these increased most rapidly among males, and may have accounted for the higher prevalences of *P. boughtoni* in males during April–May. Neither *T. pisiformis* nor *D. scapiceps* exhibited conspicuous seasonal changes in prevalence. Maximum prevalence of *T. pisiformis* was attained at about 1 yr of age, whereas *D. scapiceps* increased among adult snowshoes through age 2 yr before stabilizing. Long-term (between-year) changes in prevalence of *O. cuniculi*, *T. pisiformis*, and *D. scapiceps* were correlated significantly with the cyclic hare population which declined from a peak in fall 1961 to a low in 1965–1966, rose to another peak by fall 1970, and declined again to a low in 1975. There was no detectable time lag between this “10-yr” cycle in hare density and the cycles of parasite prevalence among juveniles (<1 yr of age). Among adult hares, the cycle of *O. cuniculi* prevalence was likewise synchronous with that of the hare population, but the cycles of *D. scapiceps* and *T. pisiformis* lagged by approximately 1 and 2 yr, respectively. This lag in *T. pisiformis* prevalence was largely inexplicable to us. Our data on *P. boughtoni* were not suitable for analyses of between-year trends; nor were those for the fifth helminth, *Taenia serialis* (coenuri), because mean prevalence was less than 1% among both juveniles and adults. An apparent decline in *T. serialis* after the early 1950's, and its continued scarcity thereafter, paralleled a major change in numbers of one important definitive host—the red fox (*Vulpes vulpes*). Lighter weights of young hares at age 37–96 days, and of adults and fully grown juveniles, were associated with *P. boughtoni* infections. There was no demonstrable relationship between snowshoe hare reproductive parameters and helminth parasitism.

INTRODUCTION

During 1961–1977 we studied a strongly cyclic snowshoe hare population near Rochester, Alberta. Over that 17-yr period 7,827 hares were necropsied, primarily to determine annual reproductive rates and population age structure. During these

necropsies we also recorded routinely the presence or absence of five parasitic helminths: *Obeliscoides cuniculi* (Graybill, 1923), *Taenia pisiformis* (Bloch, 1780), *Dirofilaria scapiceps* (Leidy, 1886), *Protostrongylus boughtoni* (Goble and Dougherty, 1943), and *Taenia serialis* (Gervais, 1847). Occurrence of all five species in the snowshoe hare had been well documented by many earlier studies; however, except for Erickson's (1944) work on *Obeliscoides* and *Taenia* in Minnesota, their prevalence in relation to the hare's cyclic fluctuations was largely unknown.

The present paper addresses this problem by examining age-specific trends in both seasonal and annual prevalence, and

Received for publication 11 July 1984.

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by collating the latter with changes in abundance of snowshoe hares. Key elements in this analysis were our knowledge of population dynamics of hares (Keith and Windberg, 1978), and our ability to (1) age juvenile hares up to 3 mo postpartum, (2) separate juveniles under 1 yr of age from adults, and (3) identify the 1-, 2- and ≥ 3 -yr age classes within the adult cohort (Keith et al., 1968; Keith and Cary, 1979). We make few direct comparisons of prevalences at Rochester with those reported from short-term studies elsewhere: the great within- and between-year differences observed by us rendered such comparisons largely meaningless.

The above mentioned five helminths have been alleged by previous investigators to cause significant pathology in snowshoes (Boughton, 1932; MacLulich, 1937; Criddle, 1938; Erickson, 1944). We have explored their impact by comparing body weights, weight gains, and reproductive parameters among parasitized vs. nonparasitized individuals. We recognize that analyses of this sort, using information on prevalence, are inherently less sensitive than those based on intensities of infection. In the host-parasite models developed by Anderson and May (1978) and May and Anderson (1978), both host and parasite demographic parameters are functions of parasite numbers per host. Our rationale for an analysis with prevalence data was simply that really major impacts by parasites on individual fitness might be detectable. Clearly, the tests of associated null hypotheses are extremely conservative.

MATERIALS AND METHODS

Snowshoe hare collections

Hares were obtained mainly (81%) by live-trapping (Keith et al., 1968); snaring (12%) and shooting (7%) provided additional samples. All were taken within 30 km of Rochester, Alberta. Live-trapped hares were usually killed and necropsied at our field laboratory on the day of capture. At that time weight, sex and age (adult

or juvenile) and other relevant field data were recorded.

Taenia serialis (coenuri)

Hare carcasses were skinned from neck to ankles prior to opening, thereby disclosing the large and conspicuous cysts of *Taenia serialis* (formerly *Multiceps serialis*; see Vester, 1969) that tend to localize in skeletal musculature. After opening, the body cavity was similarly inspected.

Dirofilaria scapiceps

To determine the presence of *Dirofilaria scapiceps* we skinned the ankle region of both hind legs, then broke open the ankle joint and examined the adjacent tendon sheath. According to Bartlett (1984a) the adult and subadult worms thus observable to us were in the synovial space between the tendon sheath and the tendons. We did not examine blood smears for circulating microfilariae.

Taenia pisiformis (cysticerci)

Immediately upon opening, the body cavity and viscera were examined for cysticerci of *Taenia* spp. We were particularly careful to check the rectal area where cysts may easily pass undetected, and the liver where they were sometimes deeply embedded. The shape, size and configuration of rostellar hooks (Vester, 1969; Bursey and Burt, 1970) in samples checked by us during 1962–1963, and in collections at Rochester overwinter 1981–1982, indicated that the observed cysticerci were *T. pisiformis*. This species also predominated in carcasses sent to the University of Alberta during 1971–1972, but some obscure cysts of *T. macrocystis* were occasionally found after intensive examination (Samuel, pers. comm.). We doubt that the latter influenced our estimates of *T. pisiformis* prevalence, and have therefore referred to *T. pisiformis* throughout this paper.

Obeliscoides cuniculi

During necropsy the stomach was opened and the mucosal surface scrutinized for adult worms. If none was evident, the ingesta were washed into a white enamel pan and also examined. We stress that these procedures detected adults chiefly, although some immatures (young 5th stage) were probably observed as they too usually lie on the mucosal surface with anteriors embedded in the mucosa (Sollod et al., 1968; Measures and Anderson, 1983a). Third- and fourth-stage larvae would not have been detected by us.

Protostrongylus boughtoni

Our main evidence of infection by *Protostrongylus boughtoni* was the presence of characteristic lesions on the lungs that were visible grossly. Such lesions have been described variously by earlier workers as “yellowish necrotic lung tissue”; “white, round, homogeneous foci (nodules)”; and “grey consolidated irregular patches” (Korthals and Shenman, 1960; Bookhout, 1971; Tobon, 1973). On many, but not all, occasions we sliced through these lesions and found worms. We did not, however, examine the lungs microscopically, and must certainly have failed to detect some infections. Our estimates of prevalence are therefore minimal, and hence constitute simply an index.

Voucher specimens of the parasites

Specimens of *Obeliscoides cuniculi*, *Protostrongylus boughtoni* and *Taenia pisiformis* (cysticerci) have been deposited in the U.S. National Parasite Collection (Beltsville, Maryland 20705, USA) and assigned Nos. 78585–78587. Specimens of *Dirofilaria scapiceps* from snowshoe hares collected in the same area in Alberta have been deposited also in the U.S. National Parasite Collection (No. 77342) by C. M. Bartlett in connection with another study (see Bartlett, 1983).

Data analysis

We used 2×2 contingency tables to test differences in prevalence by chi-square. Probabilities obtained from such tests are given in text when $P \leq 0.10$; and prevalences are said not to differ when $P > 0.10$. Possible effects of helminth presence on weight and reproduction of individual hares were assessed via appropriate multiple linear regression models for these essentially continuous responses. Presence-absence of each helminth species, as well as sex, age, season and year were encoded as indicator or “dummy” variables prior to analysis.

RESULTS AND DISCUSSION

Obeliscoides cuniculi

The life cycle of *O. cuniculi* is direct (Alicata, 1932). Non-larvated eggs passed in feces develop into infective larvae (L_3) within 7–9 days at 22 C, but require a longer time at lower temperatures (Measures and Anderson, 1983b). The prepatent period ranges from 16 to 25 days among domestic rabbits (*Oryctolagus cuniculus*) (Alicata, 1932; Worley, 1963;

Sollod et al., 1968; Measures and Anderson, 1983a), and was 17–18 days in four captive snowshoe hares (Measures and Anderson, 1983a). The latter workers recorded patency periods of 61–118 days ($\bar{x} = 81$ days) in 10 domestic rabbits, but periods exceeding 196 days have occurred following large doses of infective larvae (Worley, 1963).

Measures and Anderson (1983c) described morphological differences between *O. cuniculi* in snowshoe hares and cottontail rabbits (*Sylvilagus floridanus*) and therefore designated two subspecies—*O. c. multistriatus* and *O. c. cuniculi*, respectively. Subsequent attempts to hybridize the two subspecies were only partially successful (Measures and Anderson, 1984). Lena Measures examined some specimens from snowshoe hares from Rochester and reported that they were *O. c. multistriatus* (Measures, pers. comm.).

Seasonal prevalence: At Rochester, young snowshoes were born each year in three or four well synchronized litter groups during May–August (Cary and Keith, 1979). We sampled such young most intensively from June through August. During this period prevalence at any given age did not differ between litter groups, and we thus pooled the data to obtain an age-specific pattern of prevalence from birth to 96 days. Age was estimated from weight and hindfoot length (Keith et al., 1968) and individuals were assigned to one of eight successive age classes, each spanning 12 days.

Adult *O. cuniculi* were first observed in young snowshoes at age 17 days. Prevalence rose steeply from 12% at 25–36 days of age to 49% at 61–72 days, and thereafter increased only slightly to 53% by 85–96 days (Fig. 1). This rise in prevalence with host age was reflected likewise by an increase in mean monthly prevalence among juvenile hares from 16% in June to 46% in September (Fig. 2).

Prevalence of adult *O. cuniculi* in ju-

venile hares dropped markedly between October (43%) and November (17%) and was at its lowest during December–January (\bar{x} = 13%). There was an abrupt increase in prevalence between January (14%) and February (50%) followed by a continuous rise to 89% by May. Thus, during its first year of life the juvenile cohort experienced major seasonal changes in prevalence of *O. cuniculi*.

In our analyses, juvenile snowshoes entered the adult cohort on 1 June following their summer of birth. During June–August mean prevalence among adult hares was consistently above 90% (Fig. 2), declined to just 35% by January, but climbed steadily to rise once again above 90% by April. This conspicuous annual cycle in prevalence among adult snowshoes clearly paralleled that of juveniles from October through May.

An annual cycle based on monthly prevalences of what were apparently adult *O. cuniculi*, was earlier described in cottontail rabbits (Clancy et al., 1940) and snowshoe hares (Erickson, 1944). Neither study segregated adult and juvenile animals, and monthly samples frequently were small. Nevertheless, Erickson's (1944) data for snowshoes in Minnesota disclosed the salient features of seasonal changes in prevalence of *O. cuniculi* observed by us in Alberta, viz., a sharp decline in November from generally high levels during summer, lowest prevalences during November–January, and a large increase in February. Later studies which examined prevalence by season only also indicated that levels probably were lowest in winter among both cottontails (Dorney, 1963; Jacobsen et al., 1978) and snowshoes (Dodds and Mackiewicz, 1961).

A particularly useful aspect of Erickson's (1944) paper was its presentation of information on prevalence and intensity. In general, one would expect prevalence to reflect intensity, albeit rather insensitively. However, in Erickson's data, spanning the years 1931–1940, the correlation

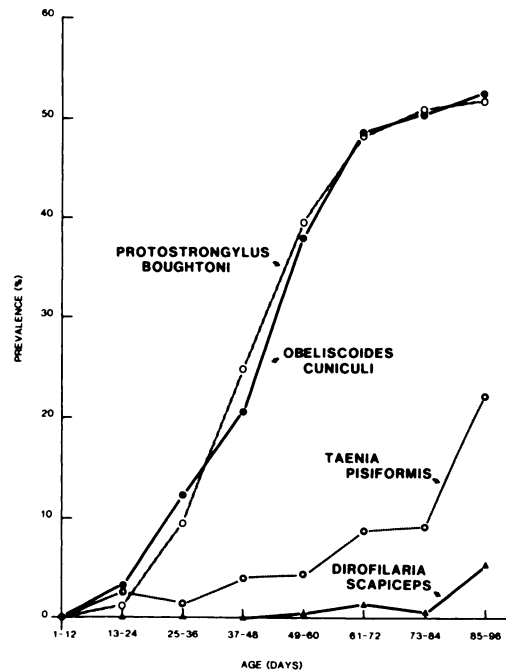


FIGURE 1. Prevalence of four helminths in juvenile snowshoe hares at 12-day intervals from birth to age 96 days, Rochester, Alberta, 1961–1977: *Protostrongylus* (n = 1,029), *Obeliscoides* (n = 1,394), *Taenia* (n = 1,556), *Dirofilaria* (n = 1,576).

between mean prevalence monthly and $\ln(\text{mean intensity monthly})$ was highly significant (r = 0.824, P < 0.01), and we therefore believe that the annual cycle in prevalence of *O. cuniculi* at Rochester was tracking a similar cycle in average intensity of infection. This view is consistent with the reported 10-fold increase in numbers of adult *O. cuniculi* in snowshoes in Ontario from January–March to April–June (Measures and Anderson, 1983d), and the approximately three-fold increase in adult worms in Maine cottontails between March and May (Gibbs et al., 1977).

Fall declines in adult worm intensity, and hence also in prevalence, have been shown to be due to arrested development of L₄ larvae in the stomach mucosa coupled with a gradual loss of adult worms throughout the patent period. The subsequent late-winter rise in intensity and

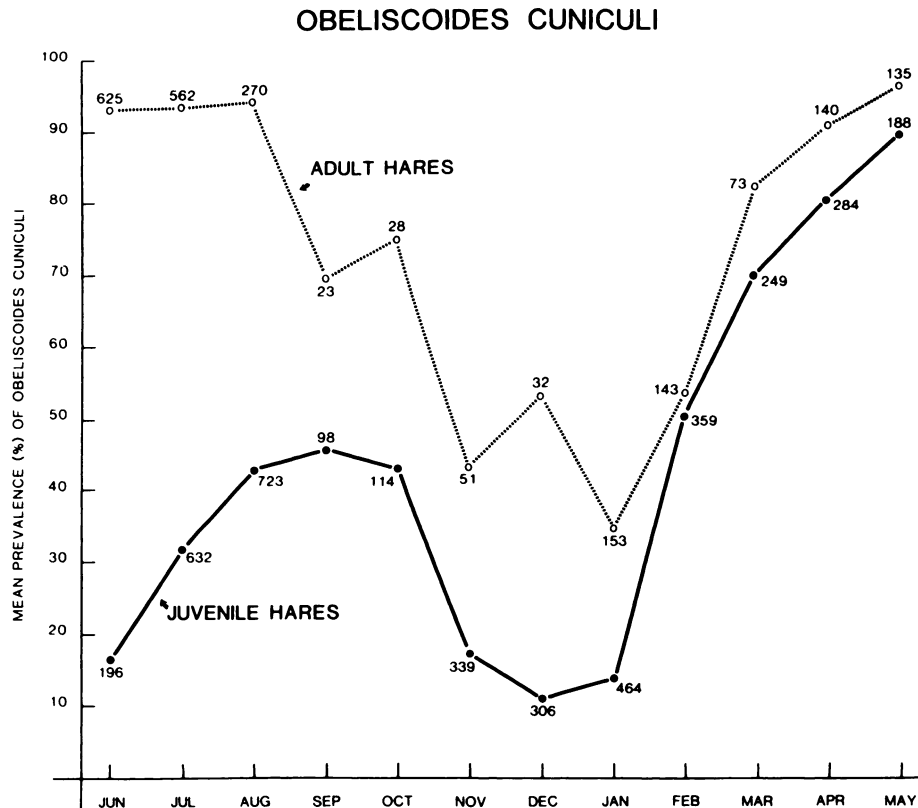


FIGURE 2. Monthly prevalence of *Obeliscoides cuniculi* in juvenile snowshoe hares during their first year of life (June to following May), and in adults thereafter, Rochester, Alberta, 1961–1977. Sample sizes are shown beside plotted values.

prevalence, well before weather conditions would normally permit reinfection (Measures and Anderson, 1983b), is caused by renewed development of the arrested L_4 larvae. Measures and Anderson (1983d), for example, found that 9% of the total population (larvae and adult worms) consisted of L_4 larvae during April–June, whereas L_4 's comprised 70% during October–December. Similarly, Gibbs et al. (1977) noted 9% L_4 's in May and 61% in December.

It has been demonstrated experimentally that exposure of infective L_3 larvae to ambient temperatures of 4 C is a highly effective means of inducing their post-ingestion arrest as L_4 's (Fernando et al., 1971; Hutchinson et al., 1972). Such tem-

peratures are common at Rochester by late August and likely trigger the major decline of adult-worm prevalence observed by us between October and November (Fig. 2). Although L_4 development can also be inhibited by host immune responses resulting from massive experimental doses (10,000–75,000) of infective larvae (Michel et al., 1975; Fox, 1976), we doubt that our hares were often so heavily exposed. It seems too that among other nematodes high adult worm densities may cause larval arrest (Gibson, 1953; Roberts and Keith, 1959; Dunsmore, 1963), but this was evidently not the case with *O. cuniculi* in wild snowshoe hares examined by Gibbs et al. (1977).

A significant decline in prevalence of

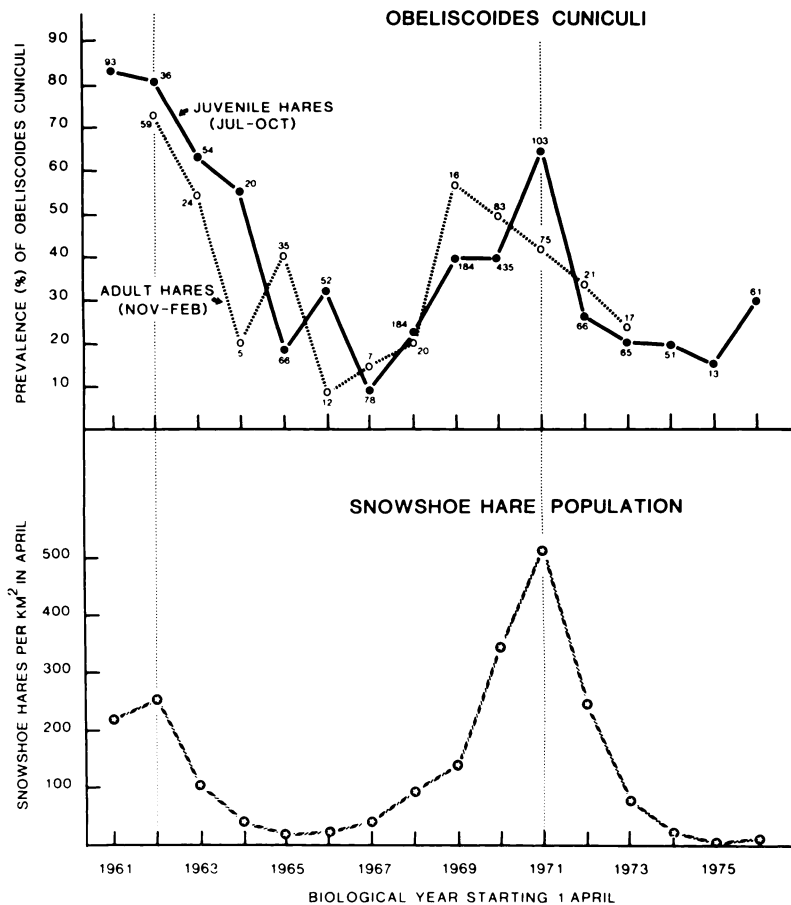


FIGURE 3. Annual prevalence of *Obeliscoides cuniculi* in juvenile and adult snowshoe hares during selected months (see explanation in text), Rochester, Alberta, 1961–1976. Sample sizes are shown beside plotted values. April snowshoe hare densities are from Keith (1983).

adult *O. cuniculi* occurred among adult hares at least 1 mo prior to the November decline among juveniles (Fig. 2). This perhaps reflects a difference in mean levels of acquired immunity resulting from the longer exposure of adult hares, and suggests that immune responses may indeed play some role in the observed fall decrease of *O. cuniculi*.

To our knowledge, the proximate cause of renewed development of L_4 larvae in February has not been determined. We note, however, that this coincided with the rapid rise in pituitary gonadotrophins and testis weights of hares preceding onset of

breeding in late March or early April (Davis and Meyer, 1972; Cary and Keith, 1979). The same general correlation clearly applies to the other snowshoe and cottontail populations cited earlier. Susceptibility of European rabbits (*Oryctolagus cuniculus*) to nematode infection was shown by Dunsmore (1966a, b, c, d) to be influenced by sex hormones, and he later reported (Dunsmore, 1971) that ACTH increased the numbers of *Trichostrongylus retortaeformis* which matured in experimental infections.

Yearly prevalence: In all years, prevalence of *O. cuniculi* among adult snow-

TABLE 1. Correlations between prevalence of three species of helminths and ln density of snowshoe hares during two cyclic fluctuations of the hare population at Rochester, Alberta.*

Helminth species	Juvenile hares				Adult hares			
	Helminth prevalence years (t)	Hare population years	r	P	Helminth prevalence years (t)	Hare population years	r	P
<i>Obeliscoides</i>	1961–1966	t	0.96	<0.01	1962–1966	t	0.84	0.07
<i>cuniculi</i>	1966–1976	t	0.62	0.04	1966–1973	t	0.80	0.02
<i>Taenia</i>	1962–1966	t	0.85	0.06	1962–1967	t – 1	0.92	<0.01
<i>pisiformis</i>	1966–1976	t	0.80	<0.01	1968–1977	t – 2	0.77	<0.01
<i>Dirofilaria</i>	1962–1966	t	0.94	0.02	1962–1967	t – 1	0.97	0.01
<i>scapiceps</i>	1966–1976	t	0.67	0.03	1967–1977	t – 1	0.77	<0.01

* Hare densities used in this analysis occurred on 1 April each year; the within-year periods from which prevalence information was utilized are given in Figs. 3, 5 and 7.

shoe hares was mostly 90–100% during April–August, and thus potentially insensitive to annual variations in intensity of infection. We therefore utilized data only from November through February where mean monthly prevalence was 35–54% (Fig. 2). With juvenile hares we used July through October data, thereby avoiding the very low and high mean monthly prevalences that followed (Fig. 2).

Between 1961 and 1977 the snowshoe hare population underwent about 1.5 cyclic fluctuations, peak spring densities occurring in April 1962 and 1971 (Fig. 3). Maximum fall densities were attained in late August 1961 and 1970 (Keith and Windberg, 1978). Because prevalences of all helminths tended to be markedly higher during the first of these hare peaks, we partitioned the data into two periods: 1961–1966 (peak to low of first cycle) and 1966–1977 (low to peak to low of second cycle).

Major long-term trends in the prevalence of *O. cuniculi* were synchronized broadly with those of the snowshoe population (Fig. 3). The correlation between prevalence and hare density was significant during both periods for juveniles ($P < 0.01$ and $P = 0.04$) (Table 1); for adults the correlation approached significance in 1962–1966 ($P = 0.07$) and was significant

in 1966–1973 ($P = 0.02$). Differences in prevalence between years of high and low hare density were pronounced among both juveniles (four- to nine-fold) and adults (two- to nine-fold). In neither age class was there any evidence of a lag between the hare and helminth cycles. This was likewise shown by Erickson (1944) who compared snowshoe densities during 1933–1939 with total annual prevalence (all ages and months) of *O. cuniculi*, and noted a concomitant maximum in each during 1935.

The direct life cycle of *O. cuniculi* exposes eggs and larvae to the vagaries of weather. Because survival of these free-living stages is probably enhanced under humid conditions (Gibbs et al., 1977; Measures and Anderson, 1983d), we tested for a relationship between prevalence and total April–August rainfall. The predictive values of the simple correlations of prevalence and hare density, summarized in Table 1, were not significantly improved ($P > 0.25$) by incorporating rainfall in a multiple-regression analysis.

Taenia pisiformis

Taenia pisiformis has a two-host life cycle, producing a larval stage (cysticercus) in rabbits and hares, the main intermediate hosts, and an adult stage in var-

TAENIA PISIFORMIS

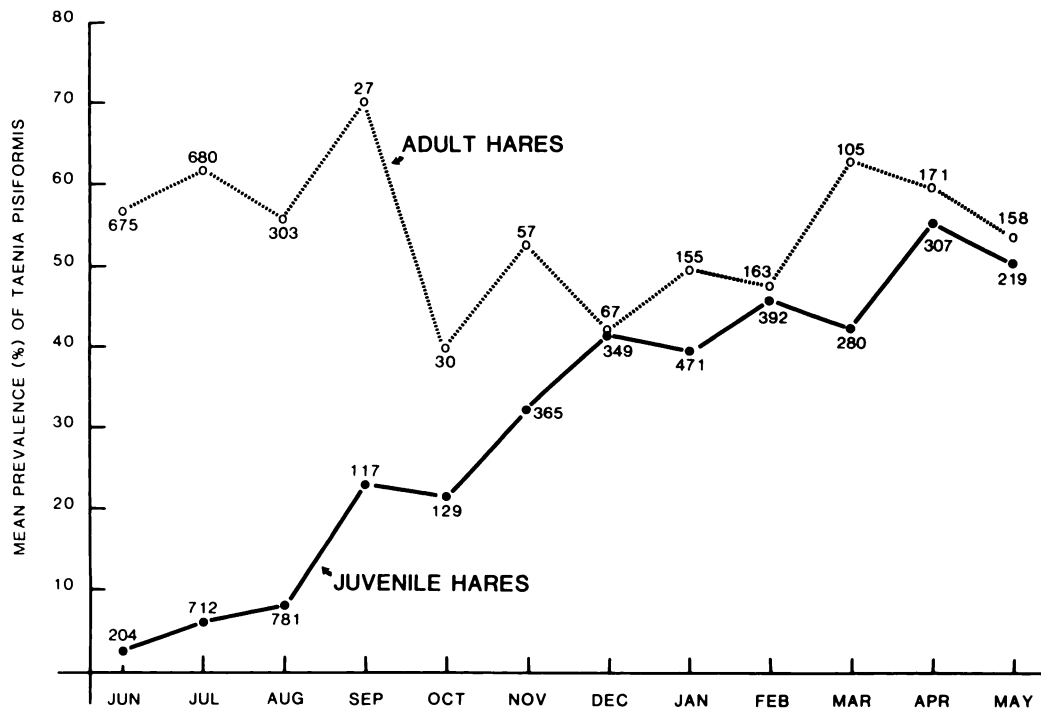


FIGURE 4. Monthly prevalence of *Taenia pisiformis* (cysticerci) in juvenile snowshoe hares during their first year of life (June to following May), and in adults thereafter, Rochester, Alberta, 1961–1977. Sample sizes are shown beside plotted values.

ious Canidae, the main definitive hosts (Abuladze, 1970). Eggs are swallowed with contaminated food or water, and oncospheres reach the portal vein within hours. Hatched activated oncospheres inoculated into the duodenum of domestic rabbits have penetrated the intestine and attained the liver within 40 min (Barker, 1970). The parasite develops in the liver and appears inside the peritoneal cavity at 14–26 days. The cysticerci are infective by day 28 (Worley, 1974). Maturation in different species of Canidae takes about 1–3 mo following ingestion of cysticerci (Abuladze, 1970).

Seasonal prevalence: We first recorded cysticerci in juvenile snowshoes at 24 days of age. Prevalence thereafter rose slowly to just 9% by age 73–84 days (Fig. 1). This slow initial increase was reflected also in

mean monthly prevalences for juveniles, which by August had reached only 8% (Fig. 4). Prevalence among juveniles by December (42%) approached that of adults, and continued upward gradually through April–May (53%).

Monthly prevalence of cysticerci in adult snowshoes fluctuated irregularly around a mean of 57% (Fig. 4). There was little evidence of any major seasonal difference, although prevalence was lower ($P < 0.01$) during October–February ($\bar{x} = 48\%$) than at other times ($\bar{x} = 59\%$). This tendency was consistent with Naumov's conclusion (Abuladze, 1970) that maximum rate of infection of "blue" hares (*Lepus timidus*) occurred in midsummer and early autumn.

Yearly prevalence: We used June–May prevalence among adult hares, and De-

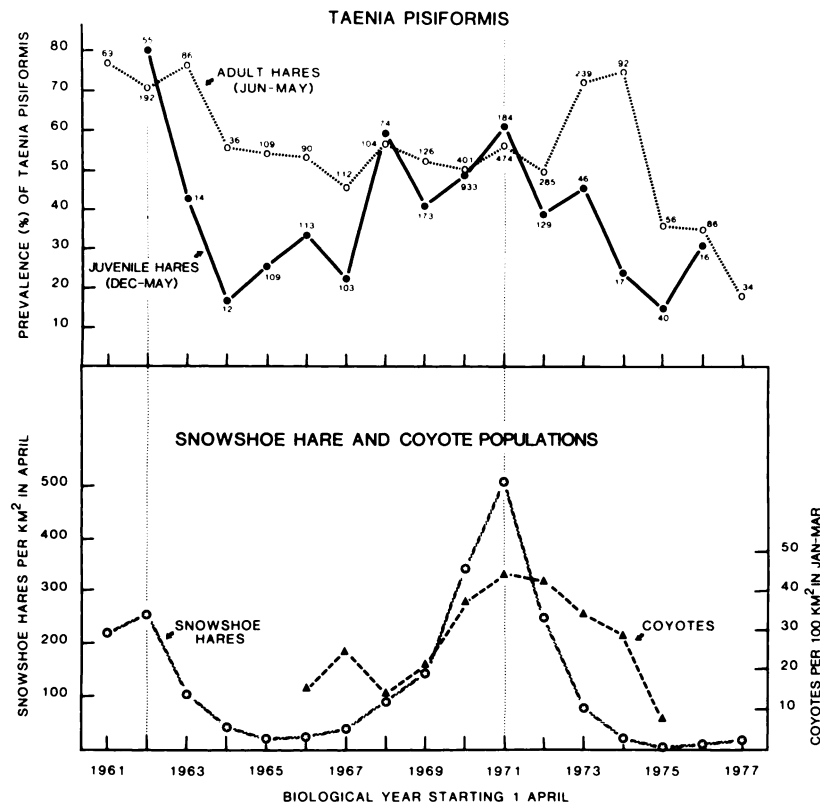


FIGURE 5. Annual prevalence of *Taenia pisiformis* (cysticerci) in juvenile and adult snowshoe hares, Rochester, Alberta, 1961–1977. Sample sizes are shown beside plotted values. April snowshoe hare densities are from Keith (1983); coyote densities are from Keith et al. (1977).

cember–May prevalence among juveniles, to track responses of *T. pisiformis* to cyclic fluctuations in snowshoe density during 1961–1977 (Fig. 5). Prevalence of cysticerci changed markedly between years or groups of years in relation to the hare cycle. For juveniles, the correlation was nearly significant in 1962–1966 ($P = 0.06$) and highly significant in 1966–1976 ($P < 0.01$) with no apparent time lag. For adults, changes in prevalence were most strongly correlated ($P < 0.01$) with hare densities 1–2 yr earlier (Table 1).

Despite the general correspondence between the prevalence of *T. pisiformis* and snowshoe abundance, large increases and decreases in density were required evidently to generate detectable changes in prevalence among adult hares. During

1964–1972, for example, prevalence varied irregularly between just 46% and 58% whereas hare density had risen 15-fold by 1970. Similarly, prevalence of *T. pisiformis* varied little during 1936–1939 (18–24%) in the Vologda region, U.S.S.R., despite approximately four-fold changes in density indices of *L. timidus* (Naumov, 1947). It was only during years of lowest populations, immediately preceding and following 1936–1939, that prevalence was appreciably less (0 and 13%). Data from Erickson's (1944) study in Minnesota, where the snowshoe hare cycle was less pronounced than at Rochester, suggested a fluctuating prevalence of *T. pisiformis* that was unrelated to hare abundance.

At this point we cannot explain why prevalence peaked so much later among

adults than juveniles. We initially hypothesized that the 3-yr difference in peak prevalence in juveniles (1971) vs. adults (1974) resulted from the increasing proportion of older animals among adults as the population declined during 1971–1974, viz., individuals ≥ 3 yr old successively comprised 18, 40, 50, and 56% of the adult cohort (Keith and Windberg, 1978). We fully expected prevalence to rise with age due to increased length of exposure, but found that there were no significant differences among 1-, 2-, and 3-yr-olds. During our study, prevalence of cysticerci in these three adult age classes averaged 58.4% ($n = 1,374$), 57.8% ($n = 381$), and 61.2% ($n = 263$), respectively. This stability might indicate that the rate of new infections approximated the disappearance rate of established infections, such disappearances resulting from differential losses of parasitized individuals or from their elimination of cysticerci. We doubt, however, that this host–parasite system was so finely tuned.

Alternatively, visible cysticerciasis may attain its maximum prevalence among 1-yr-olds (age 1 to <2 yr) and persist with age, subclinical infections having by this time immunized those other adults that are without cysticerci. Cysticerci remain viable in rabbits for 1 yr or more (Worley, 1974; Movsesyan et al., 1981) and doubtless persist much longer; host immune response to *T. pisiformis* larvae is known to be strong (Heath, 1973a, b; Rickard and Coman, 1977).

It may be noteworthy that the sharp drop in prevalence among adults in 1975 coincided with the first major reduction in numbers of coyotes (the main definitive host at Rochester) following the cyclic decline of hares 3 yr earlier (Fig. 5).

Dirofilaria scapiceps

Cottontail rabbits and snowshoe hares are the principal definitive hosts of *D. scapiceps* (Bartlett, 1983). *Dirofilaria scapiceps* is maintained within popula-

tions of snowshoe hares but appears poorly adapted. This led Bartlett (1984a) to regard the snowshoe hare as an abnormal and relatively recent host. Several species of mosquitoes (*Aedes*) serve as intermediate hosts (Highby, 1943; Bartlett, 1984b). Microfilariae circulating in the blood of rabbits or hares are ingested by mosquitoes and develop in the abdominal fat body. Infective third-stage larvae first appear in the head or labium at 11–12 days (Highby, 1943; Bartlett, 1984c). Following inoculation by feeding mosquitoes, larvae continue development in subcutaneous tissues. Subadults migrate through these tissues to the ankles, arriving there as early as day 16 (Bartlett, 1984c). Sexual maturity may be attained by day 67. Prepatent periods range from 137 to 234 days in cottontails (Bartlett, 1984c) and 286 to 391 days in domestic rabbits (Highby, 1943).

Seasonal prevalence: Our earliest record of *D. scapiceps* in juvenile hares was at age 51 days; prevalence remained below 2% throughout the first 12 wk of life (Fig. 1). Mean monthly prevalence among juveniles did not rise above 1% during June–August, but climbed rapidly thereafter to a plateau of about 36% during December–May (Fig. 6). Although subadult worms are present in the ankle region within 16 days after inoculation (Bartlett, 1984c), they are small and would not likely have been detected by us until some days later (Bartlett, pers. comm.). The leveling off of prevalence in December thus suggests that transmission probably continued into October. The highest rate of change in prevalence occurred between August (1%) and September (15%) and was consistent with Bartlett's (1984b) conclusion that transmission peaked in July and August.

The stability in mean prevalence among juvenile snowshoes from December through May, following cessation of transmission, indicates that survival of adult worms commonly exceeds 6 mo in the

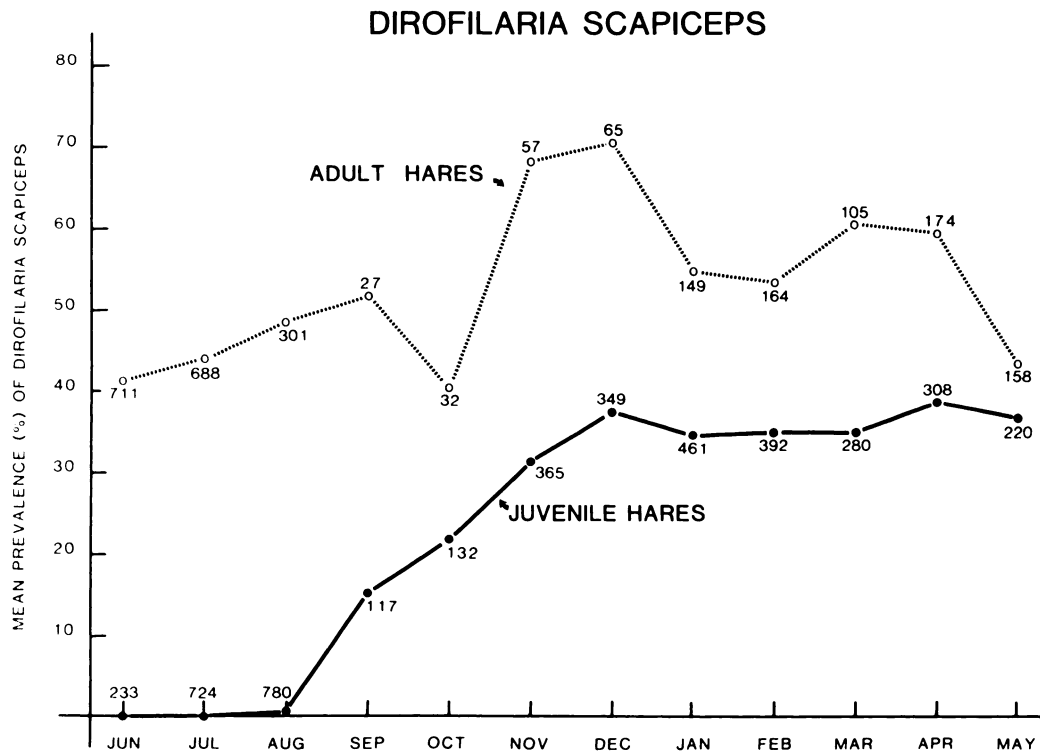


FIGURE 6. Monthly prevalence of *Dirofilaria scapiceps* in juvenile snowshoe hares during their first year of life (June to following May), and in adults thereafter, Rochester, Alberta, 1961–1977. Sample sizes are shown beside plotted values.

wild. This would seem essential for maintenance of the parasite because mosquitoes were never noticeably abundant at Rochester before late May. Highby (1943) reported that no adults were recovered from two experimentally infected domestic rabbits by 353 and 421 days postinoculation, but Bartlett (1984c) mentions adult worms in cottontails at day 790. Adults of a closely related filariid, *C. uniformis*, may be retained in cottontails for more than 2 yr (Bray and Walton, 1961). It is therefore highly probable that primary infections from the first summer and fall of life persist well into the second. Furthermore, Bartlett (1984c) successfully reinfected cottontails in which adults from primary infections were still present. Any immune response had therefore been insufficient to afford complete protection. In

light of the above, one would predict a significant rise in prevalence during the second year of life. This did indeed happen, the 36% ($n = 2,010$) for juveniles in December–May increasing to 56% ($n = 423$) for 1-yr-olds during these same months 1 yr later ($P < 0.01$). A balance between rates of infection and elimination must by then have been effected as no further increase occurred among 2-yr-olds (55%, $n = 128$) or ≥ 3 -yr-olds (60%, $n = 114$).

Mean monthly prevalence among adult hares ranged between 41% and 71%, tending to increase from June through December, then to decrease through May (Fig. 6). A closer inspection of our data showed that the June–December rise was restricted within the adult cohort to 1-yr-olds, and accounted for the previously noted

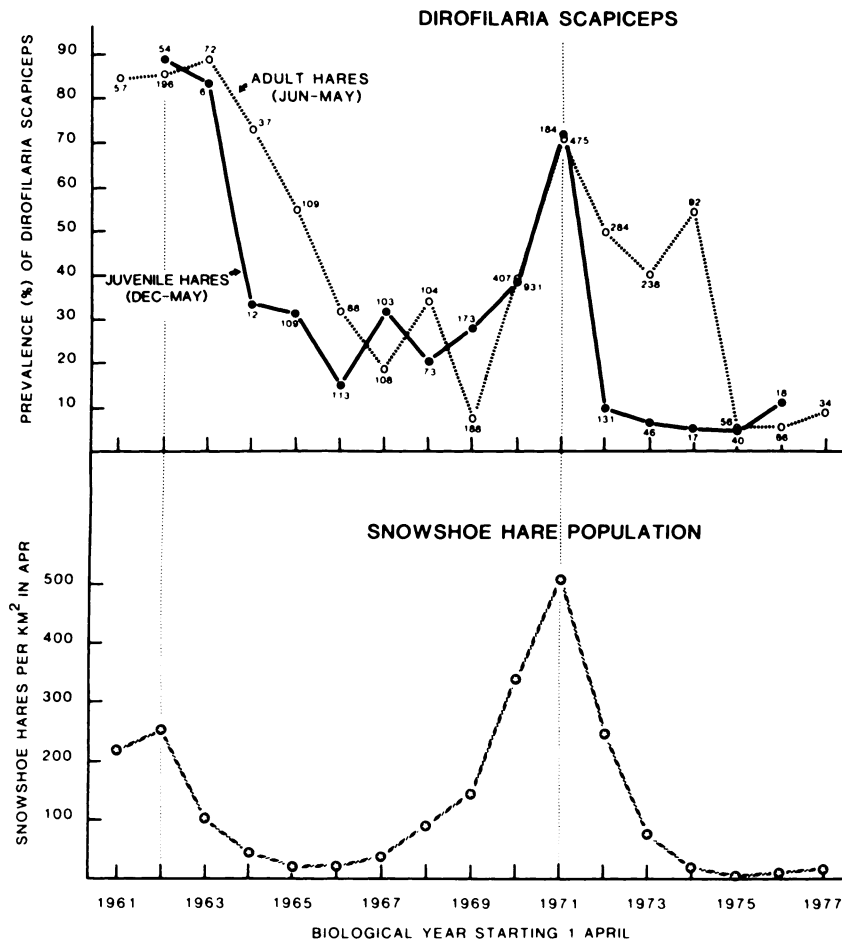


FIGURE 7. Annual prevalence of *Dirofilaria scapiceps* in juvenile and adult snowshoe hares, Rochester, Alberta, 1961–1977. Sample sizes are shown beside plotted values. April snowshoe hare densities are from Keith (1983).

difference between prevalence in 1-yr-olds vs. juveniles during December–May.

Yearly prevalence: Annual changes in prevalence of *D. scapiceps* among both juvenile and adult hares (Fig. 7) were significantly correlated with cyclic changes in hare density (Table 1). Prevalence in juveniles (December–May) tended to reflect hare density trends directly, whereas with adults (June–May) the strongest correlations were obtained using a 1-yr lag. The latter would be expected if, as concluded earlier, infections persist more than a year and host immune response is weak.

Because mosquito populations were not monitored by us, we can say little about their short-term effect on prevalence of *D. scapiceps*. However, mosquitoes were notably more abundant during wet summers, and many *Aedes* spp. important in transmitting *C. scapiceps* depend on snowmelt pools in early spring (Bartlett, pers. comm.). Thus we explored through multiple regression the influence of total April–August rainfall and overwinter snowfall on prevalence of *D. scapiceps*. Neither of these variables significantly increased ($P > 0.15$) the predictability of

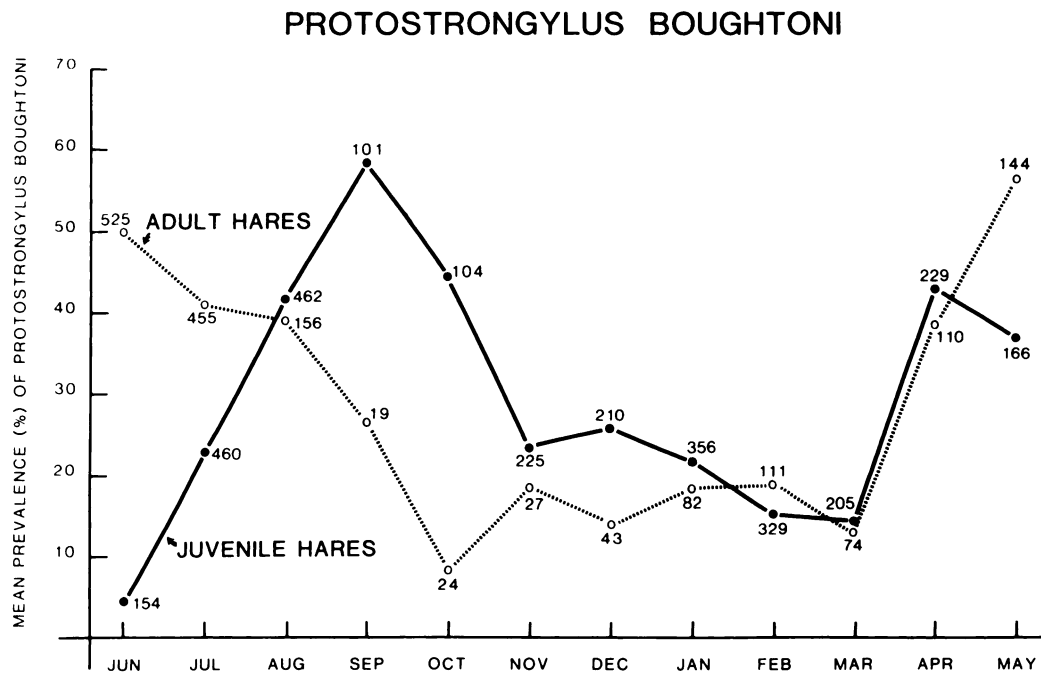


FIGURE 8. Monthly prevalence of *Protostrongylus boughtoni* in juvenile snowshoe hares during their first year of life (June to following May), and in adults thereafter, Rochester, Alberta, 1965–1977. Sample sizes are shown beside plotted values.

prevalence over that provided by hare density alone.

Protostrongylus boughtoni

The lungworm, *P. boughtoni*, is found apparently throughout the geographic range of the snowshoe hare, its definitive host (Goble and Dougherty, 1943; Kralka, 1983). Several species of valloniid and pupillid snails serve as intermediate hosts for the larval stages which complete two molts to become L_3 's in 28–30 days (Kralka and Samuel, 1984). Adult worms appeared in the lungs of an experimentally infected snowshoe within 17 days (Kralka and Samuel, 1984), and in wild young at minimum ages of 18 days (Tobon, 1973) and 23 days (Kralka, 1983). Prepatent and patent periods range from 25 to 27 days and 41 to 104 days, respectively, with maximum output of L_1 's in hare feces at 12–23 days into the patent period (Kralka and Samuel, 1984).

Seasonal prevalence: As indicated in the Materials and Methods section, the following estimates of prevalence are minimal and thus only provide indices to trends.

We first saw lungworms in snowshoes at 18 days of age; by 25–36 days prevalences averaged 9% (Fig. 1). These were early post-partum infections, as there is no evidence of transplacental transmission in *P. boughtoni* (Tobon, 1973; Kralka, 1983). Prevalence increased rapidly up to age 61–72 days (49%) and then stabilized—73–84 days (51%), 85–96 days (52%). Mean monthly prevalences in the juvenile cohort peaked at 58% during September, and fell sharply to 23% by November (Fig. 8). A slow but significant ($P = 0.03$) decline thereafter reduced prevalence to 15% by February. Between March and April, prevalences rose abruptly from 18% to 43% (Fig. 8). The above noted birth-to-November changes in prevalence were paralleled by changes in intensity during

1981 on a study area 130 km northwest of Rochester (Kralka, 1983).

A well defined seasonal cycle in prevalence was also evident among adult hares (Fig. 8). There was a continuous drop from 50% in June to a mean of 14% by October–November. Mean monthly prevalence did not change from October to March, averaging just 16%. As with juveniles, a sharp increase took place in April (38%). Mean prevalences among adults peaked in May at 56%. A similar seasonal cycle occurred in *Protostrongylus* spp. infections of *L. timidus* in the Vologda region, U.S.S.R.: there, bimonthly intensities rose markedly from January–February to March–April, peaked during May–June, and then declined (Naumov, 1947).

Prevalence in 1-yr-old snowshoes (41%, $n = 1,033$) did not differ ($P > 0.10$) from that in 2-yr-olds (45%, $n = 264$), but a decline occurred ($P = 0.04$) among individuals ≥ 3 yr old (36%, $n = 211$) which was perhaps indicative of an immune response.

The marked fall declines in prevalence among adults (September and October) and juveniles (October and November) resembled those caused by larval arrest in *Obeliscoides cuniculi* as described earlier. Kralka (1983) found L_4 's in greatest abundance in lungs of adult snowshoes during winter, and suggested that these larvae were likely arrested because both direct transmission and winter infection from intermediate hosts were highly improbable. Such arrest, coupled with the rapid post-patent disappearance of adult worms (Kralka, 1983), could account for the abrupt drops in prevalence observed by us in fall. Samuel (pers. comm.) has suggested to us that this decrease in prevalence was probably more apparent than real, viz., a reduction in visible lesions with reduced intensities of infection, but with actual prevalence remaining constant at 100% as recorded by Kralka (1983). Kralka's method of detecting infections of *P. boughtoni* was far more sensitive than ours, and indicated that prevalence

reached 100% among juveniles by August and never declined thereafter.

The major rise in prevalence among both adult and juvenile snowshoes from March to April at Rochester likely reflects, in part, renewed development of arrested larvae, a consequence of which would be an increase in lesions. The latter, which we often used as the sole indicator of prevalence, might have increased also in both number and conspicuousness if onset of reproduction stressed the immune system (Esch et al., 1975; Samuel, pers. comm.). The ground was usually snow-covered and frozen through mid-April, thus largely negating the possibility of larval transmission from intermediate host snails up to that time. The 2–3 wk required after transmission for adult worms to be present in lungs of hares would place detectable new infections well into May.

We pointed out that renewed development of arrested larvae of *O. cuniculi* in February coincided with the seasonal rise in pituitary gonadotrophins. Renewed development of *P. boughtoni* larvae evidently occurred 2 mo later, at the outset of the breeding season (Cary and Keith, 1979). Follicle-stimulating hormone (FSH) and luteinizing hormone (LH) levels would have been even higher then (Davis and Meyer, 1972), as would circulating gonadal androgens and estrogens.

Yearly prevalence: Because lungworm infections were not systematically recorded in some years, and searched for with varying intensity in others, we did not feel that meaningful year-to-year comparisons of prevalence were possible. Cary and Keith (1979), however, used this same data set to compare annual prevalence of *P. boughtoni* among pregnant females with a 10-yr oscillation model. They found no significant oscillation in prevalence ($P = 0.21$).

Taenia serialis

The adult stage of this tapeworm occurs primarily in Canidae where it probably matures within 1–3 mo and persists for a

year or more (Abuladze, 1970). Eggs passed in canid feces are ingested by rabbits or hares, the obligate intermediate hosts. Digestive processes release the hexacanth which penetrate the intestinal wall and enter the blood stream (Meyer, 1955). These may subsequently lodge anywhere in the body, but coenuri (cysts) most frequently develop in subcutaneous and intermuscular connective tissue and skeletal musculature (Meyer, 1955; Abuladze, 1970). Coenuri are apparently infective to definitive hosts after 2–3 mo, and may survive in intermediate hosts for up to 2 yr (Abuladze, 1970).

Prevalence: During 1961–1977 *T. serialis* was rarely encountered at Rochester. Prevalence was 0.1% ($n = 4,360$) among juvenile snowshoes through 1 yr of age and 0.8% ($n = 2,656$) among adults. We suspect this extremely low prevalence of *T. serialis* in our hares was a recent development. One of us (Keith) assisted the late William Rowan with snowshoe hare studies in Alberta during 1950–1953 when the conspicuous cysts of *T. serialis* were commonly encountered. It was largely because of such coenuriasis (often termed “blisters” by the early settlers) that snowshoes are still seldom eaten in the Prairie Provinces. Prevalence of *T. serialis* in Alberta up to the mid 1950’s was probably akin to the 6–16% reported in Minnesota and Manitoba during the 1930’s (Boughton, 1932; Erickson, 1944). Prevalence in large samples of Arctic hares (*Lepus timidus*) in the USSR has ranged mainly between 3 and 10% (studies summarized by Abuladze, 1970).

The apparent decline of *T. serialis* between the early 1950’s and 1960’s, and its extreme scarcity thereafter, was concomitant with the disappearance of red foxes from large sections of Alberta. At Rochester we saw neither foxes nor fox tracks in 17 yr of intensive field work including aerial counts of hares, coyotes (*Canis latrans*) and white-tailed deer (*Odocoileus virginianus*). The fox population crash from a high in 1951–1952 (Rowan, 1954)

was associated with three events: a cyclic decline of snowshoe hares (Keith, 1963), a rabies epidemic centered in foxes, and a rabies control program that reportedly killed 55,000 foxes in 2.5 yr (Ballantyne, 1958). Subsequent failure of the fox population to recover coincided with a major increase in distribution and abundance of lynx (*Lynx canadensis*) (Brand and Keith, 1979; Todd and Geisbrecht, 1979)—an event likely triggered by the unprecedented low in fur prices, and hence in trapping pressure, that occurred during 1948–1958.

Sex-specific prevalence

We have previously outlined and compared monthly and yearly trends in helminth prevalence among different age classes of hares. Our analyses also included an examination of such trends by sex, and it is this subject that we now address.

Time-specific (monthly and annual) prevalences of *Obeliscoides cuniculi*, *Taenia pisiformis*, and *Dirofilaria scapiceps* did not differ significantly ($P > 0.10$) between male and female snowshoes. Overall prevalences during 1961–1977 were as follows: *O. cuniculi*—adult male 83.7% ($n = 1,154$), adult female 84.9% ($n = 1,074$); juvenile male 38.4% ($n = 1,957$), juvenile female 39.6% ($n = 1,992$). *Taenia pisiformis*—adult male 56.6% ($n = 1,340$), adult female 56.7% ($n = 1,251$); juvenile male 28.3% ($n = 2,140$), juvenile female 27.2% ($n = 2,183$). *Dirofilaria scapiceps*—adult male 47.4% ($n = 1,355$), adult female 48.5% ($n = 1,276$); juvenile male 20.1% ($n = 2,161$), juvenile female 21.1% ($n = 2,187$).

Erickson (1944) reported that prevalence of *O. cuniculi* was similar among male and female snowshoes ($n = 714$) in Minnesota; and Measures and Anderson (1983c) indicated that mean intensity was similar between the sexes in both adult snowshoes ($n = 64$) and cottontails ($n = 60$) in Ontario. However, Gibbs et al. (1977) found a 50% higher intensity ($P <$

0.05) among adult female snowshoes ($n = 140$) during March–May in Maine.

In neither Boughton's (1932) sample of snowshoe hares ($n = 288$) from Manitoba, nor in Erickson's (1944) sample ($n = 772$) from Minnesota, did prevalence of *T. pisiformis* differ between the sexes. Similar prevalence of *T. pisiformis* in male and female cottontails was likewise reported from Connecticut ($n = 314$) (Clancy et al., 1940) and Iowa ($n = 171$) (Vande Vusse, 1969). The latter investigator ascribed the higher prevalence noted among male cottontails by Berg and Beck (1968) in New York to an inadequate sample ($n = 53$).

To our knowledge, previous studies have not examined prevalence of *D. scapiceps* by sex.

In contrast to the above three helminths, there was a significant difference ($P = 0.04$) in overall prevalence of *Protostrongylus boughtoni* between adult males (41.6%, $n = 961$) and adult females (36.7%, $n = 809$) at Rochester. A closer inspection of the data showed that this was due *entirely* to a marked sex-specific difference during April–May, when prevalence averaged 65% ($n = 124$) among males and just 36% ($n = 130$) among females ($P < 0.001$). The same trend was evident but less pronounced among juveniles, prevalence during April–May averaging 44% ($n = 203$) in males and 36% ($n = 191$) in females ($P = 0.10$). The difference between adult and juvenile males, 65% vs. 44%, was highly significant ($P < 0.001$).

We concluded earlier that because snow cover is usual through mid-April at Rochester, new infections from ingestion of intermediate-host snails would not likely appear until May. We likewise noted that the March to April rise in apparent prevalence matched the annual onset of breeding by snowshoes, and thus elevated levels of gonadal androgens and estrogens. To explain the April–May difference in prevalence between males vs. females, and be-

TABLE 2. Progression of spring coat-color change among male and female snowshoe hares, Rochester, Alberta, 1961–1977. Samples sizes in parentheses.

Interval	% of hares white or mostly white		P
	Males	Females	
16–31 Mar	99 (101)	99 (102)	
1–15 Apr	79 (182)	62 (159)	<0.001
16–30 Apr	12 (669)	4 (659)	<0.001
1–15 May	6 (133)	1 (139)	0.02
16–31 May	1 (129)	1 (105)	

tween adult vs. juvenile males, we now hypothesize that (1) renewed larval development and/or critical stress on the host immune system is triggered when circulating gonadal hormones reach a threshold level, (2) this level is attained in males before females, and (3) in adult males before juvenile males.

There were no direct measurements of hormone levels with which to test parts (2) and (3) of the above hypothesis. However, indices to chronological changes in circulating gonadal hormones (Lincoln, 1974) were available from testis and ovary weights during recrudescence, and from information about onset of breeding. As a general rule among hares, males come into breeding condition before females (Flux, 1981). For example, Bookhout (1965) found that earliest spermatogenesis preceded earliest conception in snowshoes by 6 wk; and testis weights of Arctic hares rise more rapidly and peak 1 mo earlier than ovary weights (Naumov, 1947; Naumov and Orlov, 1960). Among male snowshoe and Arctic hares, testis weights of adults consistently exceed those of juveniles throughout the January–May period of testicular recrudescence (Newson, 1964; Flux, 1970; Keith, unpubl. data). These observations support the idea that gonadal hormone levels increase in males before females, and are higher in adult males than in juvenile males.

The sex-specific difference in April–

May prevalence of *P. boughtoni* might, alternatively, have been due to higher levels of circulating pituitary gonadotrophins among males during March–April. To test that hypothesis we compared the chronological progression of the spring molt in male and female snowshoes at Rochester. This molt is wholly evoked by rising pituitary gonadotrophins and is independent of gonadal hormones (Lyman, 1943). There was no difference between the sexes from January through March: 99% of both males and females were still white or mostly white as late as 16–31 March. Subsequently, however, the color change progressed at a faster rate among females (Table 2). Flux (1970) reported a similar situation with Arctic hares in Scotland, and Severaid (1945) found that female snowshoes molted earlier and more rapidly than males in Maine. If the postulated sex-specific difference in gonadotrophin levels had been responsible for the observed sex-specific difference in *P. boughtoni* prevalence, then males, not females, should have molted most rapidly.

Body weight and parasitism

To test the hypothesis that young hares are adversely affected by parasitism, we compared weights of parasitized and unparasitized individuals through 96 days of age. These young were aged from eye-lens weights (Keith et al., 1968), and a stepwise multiple linear regression was used to assess the impacts of the four common helminths on body weight. We found no significant effect of *Obeliscoides cuniculi*, *Taenia pisiformis*, or *Dirofilaria scapiceps* on age-specific weights of young hares. However, lower weights were associated with the presence of *Protostrongylus*. During 37 to 96 days of age, individuals with *P. boughtoni* infections averaged 4.8% ($P < 0.02$) lighter than those without (Fig. 9).

We next explored the possible relationship between parasitism and weights of

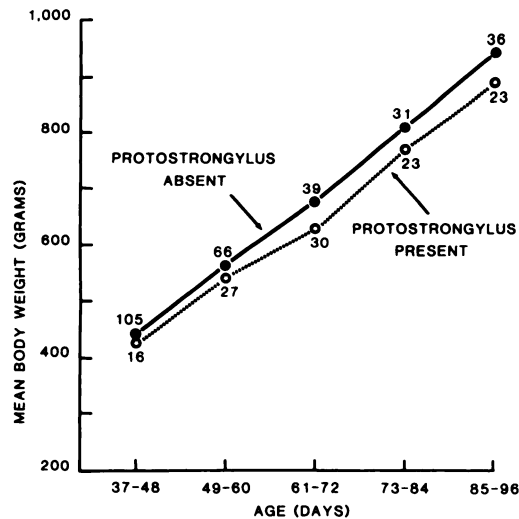


FIGURE 9. Trends in mean weights of juvenile snowshoe hares with and without *Protostrongylus boughtoni* infections. Weights of infected individuals averaged 4.8% less ($P < 0.02$) than uninfected ones over the five 12-day intervals between age 37 and 96 days. Sample sizes are shown beside plotted values.

adult and juvenile males and females. Once again it was *P. boughtoni* with which lower body weights were significantly associated (three of the four sex-age classes). On average, infected individuals were 52 g (3.9%) lighter (Table 3). In contrast, heavier body weights were associated with the presence of *Obeliscoides cuniculi* in adult females ($P < 0.02$) and *Dirofilaria scapiceps* in adult males ($P < 0.001$) and juvenile females ($P = 0.07$). We have no explanation for these latter relationships, but our analyses indicated no significant interaction among the four helminths with respect to influence on weight.

There is a strong inference in the foregoing that *P. boughtoni* has a negative impact on weight gains and mean weights of snowshoe hares. We suspect this may be translated demographically into decreased rates of survival because lighter weight individuals have higher disappearance rates (Keith and Windberg, 1978).

TABLE 3. Relationship between body weight and parasitism among snowshoe hares at Rochester, Alberta, 1961–1977.*

		Difference in mean body weight of parasitized vs. unparasitized hares and associated levels of statistical significance			
Parasite		Adults		Juveniles	
		Males (Jun–May)	Females (Sep–Apr)	Males (Nov–Apr)	Females (Nov–Apr)
<i>Protostrongylus boughtoni</i>	Av. diff. (g)	–37	–55	–45	–72
	% diff.	–2.9	–3.7	–3.6	–5.4
	P	<0.01	NS ^b	<0.01	<0.001
<i>Obeliscoides cuniculi</i>	Av. diff. (g)	+24	+95	+11	–6
	% diff.	+1.9	+6.7	+0.9	–0.5
	P	NS	0.02	NS	NS
<i>Taenia pisiformis</i>	Av. diff. (g)	–9	–25	+9	–10
	% diff.	–0.7	–1.7	+0.7	–0.7
	P	NS	NS	NS	NS
<i>Dirofilaria scapiceps</i>	Av. diff. (g)	+49	0	+7	+25
	% diff.	+3.9	0	+0.6	+1.9
	P	<0.001	NS	NS	0.07

* Months used in this analysis were selected to reduce variance in weight due to pregnancy of adult females and growth of juveniles. Differences and probabilities were determined through forward stepwise multiple linear regression.

^b $P > 0.10$.

On the other hand, a year-by-year analysis of weight differences accountable to *P. boughtoni* disclosed no apparent relationship with the hare's cyclic fluctuation. Earlier workers in both North America and the Soviet Union have described extensive pathological changes and evident respiratory impairment accompanying *Protostrongylus* infections in hares. They likewise suggested that the consequences of such parasitism would be reflected at the population level, but provided no direct evidence of this (Boughton, 1932; Erickson, 1944; Naumov, 1947, 1960; Tobon, 1973).

Reproduction and parasitism

Snowshoe hares at Rochester had a maximum of either three or four litters annually. The closely synchronized onset of first conceptions each year, and subsequent matings immediately postpartum, resulted in distinct litter groups. To test the hypothesis that reproduction was depressed by parasitism, we compared first-litter conception dates, ovulation rates

(number of corpora lutea), litter sizes (number of viable embryos in utero), and pregnancy rates among parasitized vs. unparasitized females of breeding age (≥ 8 mo old). All four reproductive parameters varied cyclically with the hare population, and the latter three differed markedly between litter groups within years (Cary and Keith, 1979). This necessitated a statistical design that nested potential endoparasite effects within both years (according to population trend) and litter groups (first through fourth). We used a stepwise multiple linear regression model for analyses of ovulation rates, litter sizes, and conception dates; and a log-linear model for pregnancy rates.

No significant effects of parasitism were suggested by our analyses. Since we are reporting negative results, it seems appropriate to indicate the sensitivity of these tests given available sample sizes. Expressed in terms of least significant differences, parasite effects would have been detectable if they had accounted for percentage changes of at least the following

magnitude: 15% in number of corpora lutea and viable embryos, 10% (2 days) in first-litter conception date, 20% in third- or fourth-litter pregnancy rate.

ACKNOWLEDGMENTS

The long-term research program near Rochester, Alberta, that generated our data was funded by a series of NSF, NIH, government, university and private grants. Besides ourselves, a number of technicians and graduate students participated in this program. Both the supporting agencies and the personnel were fully acknowledged by Keith and Windberg (1978) and Zarnke and Yuill (1981). The initial draft of this paper was examined by W. M. Samuel, R. A. Kralka, R. C. Anderson, L. N. Measures, and C. M. Bartlett. We are grateful for their helpful suggestions.

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