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INTERACTION OF THE TICK (*HAEMAPHYSALIS LEPORISPALUSTRIS*) WITH A CYCLIC SNOWSHOE HARE (*LEPUS AMERICANUS*) POPULATION

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ABSTRACT: Prevalence and intensity of the tick, *Haemaphysalis leporispalustris*, were monitored during 1963 to 1976 in a cyclic snowshoe hare (*Lepus americanus*) population near Rochester, Alberta, Canada. Prevalence was near zero from December through March, and near 100% among adult hares from May through September. Prevalence among juvenile hares approached 100% by age 2 mo. Intensity peaked for both adults and juveniles during May–June and again in August. Mean intensities were significantly higher among adult males than adult females in 5 of 13 yr, and almost significant in two others. Tick intensities were lowest during 3 yr, 1969 to 1971, when hare densities were highest. Tick intensities in spring were correlated with intensities the previous fall. Survival of marked adult and juvenile hares was unrelated to intensities of infestation. Mean numbers of corpora lutea and embryos tended to be lower among adult females with heavy tick infestations, and intra-uterine losses rose steadily from about 3 to 13% as tick intensities increased from none to heavy. Comparison of average tick intensities on adults 1-, 2-, and ≥3-yr-old yielded no evidence of increased immunity with age.
Key words: Snowshoe hare, *Lepus americanus*, ticks, *Haemaphysalis leporispalustris*, cycles, prevalence, intensity, host-parasite interactions.

INTRODUCTION

During 1961 to 1977, we studied a population of snowshoe hares (*Lepus americanus*) near Rochester, Alberta, Canada. Our primary objective was to determine how the cyclic fluctuations, which characterize snowshoe hare populations throughout most of Canada and Alaska, are generated. This research focused on hare demography and those factors (food, predators and weather) whose influence on hare survival and reproduction seemed paramount (reviewed by Keith, 1990). A further aspect of the Rochester hare study was arbovirus research that attempted to assess the role of *Haemaphysalis leporispalustris* as a vector (Hoff et al., 1971). The latter work involved collection of ticks from live-trapped hares, and led to our routinely recording tick prevalence and intensity during 1963 to 1976.

In the present paper, we document seasonal and annual changes in tick abundance over a complete hare cycle, examine the influence of hare density on intensity of infestation and test for tick-related effects on the hare population.

Haemaphysalis leporispalustris is a three-host tick, family Ixodidae, that is widely distributed in North America from Alaska well into Mexico (Bishopp and Trembley, 1945). Although primarily a parasite of wild rabbits and hares (Leporidae), its nymph and larval stages often infest other small mammals and several species of birds (Green et al., 1943; Bishopp and Trembley, 1945; Brown and Kohls, 1950). This tick only rarely engorges on humans (Brown, 1945).

Adult female *H. leporispalustris* deposit single masses of about 300 to 3,000 eggs on the soil surface or under debris, then die (Campbell and Glines, 1979). The time required for development and maturation of eggs, larvae and nymphs is importantly dependent on ambient temperatures. Whereas two generations may occur annually in the southern United States (Farlow et al., 1969), a single life cycle reportedly takes two years in Nova Scotia's colder summers (Campbell et al., 1980). After engorging, larvae and nymphs drop off their host, molt and await a new host. All four stages may overwinter, but adults and nymphs most commonly do so (Mohr

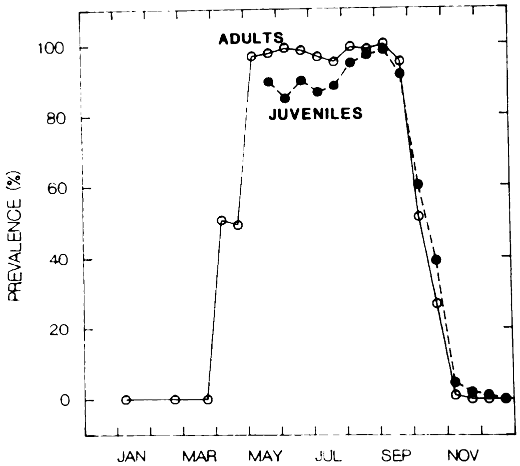

FIGURE 1. Mean prevalence of ticks (*Haemaphysalis leporispalustris*) on 4,082 adult and 3,884 juvenile snowshoe hares at semi-monthly intervals during 1963 to 1976. The minimum number of adult or juvenile hares examined in any plotted semi-monthly interval was 20.

and Lord, 1950; Campbell et al., 1980). Green et al. (1943) noted that the use of forms and dusting sites by snowshoe hares facilitates tick transmission. Engorged *H. leporispalustris* drop off the hares mainly during daylight (Campbell et al., 1980), when forms and dusting sites are most apt to be occupied.

METHODS

Study region

Information on tick prevalence and intensity was obtained from snowshoe hares live-trapped within approximately 10 km of Rochester, Alberta, Canada (54°23′N, 113°27′W). There were four intensive study areas on which hare population demography was closely monitored without removal (Keith and Windberg, 1978) and numerous other sites from which hares were collected for post-mortem examination.

The region is about two-thirds forested, with aspen (*Populus tremuloides*) dominating heavier soils, jackpine (*Pinus banksiana*) on sandy areas, and black spruce (*Picea mariana*) in scattered bogs. Recurrent wild fires have largely prevented succession to a white spruce (*Picea glauca*) climax on uplands. The climate is northern continental: annual precipitation (water equivalent) averages 45 cm, one-third of which is snow. July and January mean temperatures are 17 and −16 C, respectively.

Field procedures

Snowshoe hares were taken in 23 × 23 × 61 cm National live traps (National Liver Trap Corp., Tomahawk, Wisconsin 54487, USA) set on well used runways. Traps were baited with alfalfa hay in fall, winter and spring, but unbaited in summer. Hares caught on the four intensive study areas were sexed, aged (adult or juvenile), weighed, permanently marked and released immediately at the trap site. During April to August adult females were palpated for pregnancy. These and other relevant field techniques are fully described by Keith et al. (1968).

Rating of tick intensity

Intensities of infestation used in the present analysis were obtained in the field and laboratory from live hares only. All stages of *H. leporispalustris* tend to concentrate on the head and are especially conspicuous on the ears, muzzle and around the eyes. We did not attempt to distinguish between larval, nymph and adult ticks, nor to obtain total counts, but examined the head of each hare and rated intensity on a scale of 0 to 5 (none present to very heavy infestation) using the following criteria: 0, none present; 1, very few, one to five ticks; 2, few, six to about fifteen ticks, mostly on ears; 3, moderate, ears up to 10% covered with ticks and some present elsewhere on head; 4, heavy, ears 10 to 50% covered with ticks and many present elsewhere on head; 5, very heavy, ears >50% covered with ticks and many present elsewhere on head.

Note that hares given an intensity rating of 5 were infested with at least several hundred ticks. Mean intensity ratings (intensity indices) reported later by us for various sex and age classes or years include only individuals with ticks; those with intensity ratings of 1 to 5.

RESULTS

Prevalence

Ticks were not found on adult (age >1 yr) snowshoe hares after mid-November, nor on juveniles after mid-December (Fig. 1). Ticks next appeared in early April when prevalence rose sharply to about 50%. Thereafter, prevalence on adults was 95 to 100% through September, then declined abruptly to 27% by late October.

Appreciable numbers of young hares were initially caught in live traps during the latter half of May when mainly 3- to 5-wk-old. By that time, prevalence among these first-litter individuals was already

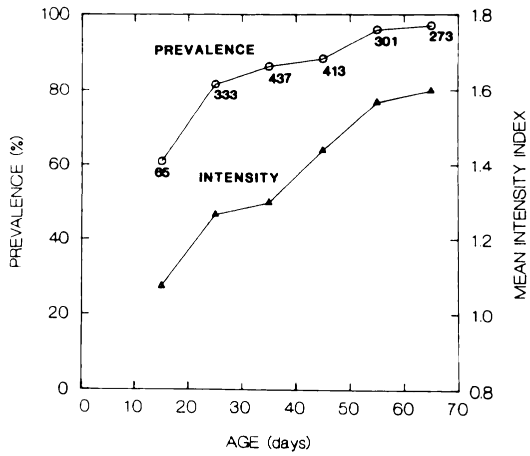

FIGURE 2. Age-related increases in mean prevalence and intensity of ticks (*Haemaphysalis leporispalustris*) on young snowshoe hares during 1963 to 1976. The number of hares examined within each 10-day age interval is shown below the prevalence plot. See text for description of intensity index.

near 90% (Fig. 1). Two or three additional litters were born to adult females each year (Cary and Keith, 1979), and overall prevalence among young trapped during June to September ranged from 85% to 98%. As among adults, prevalence declined abruptly during October—averaging just 5% during the first half of November.

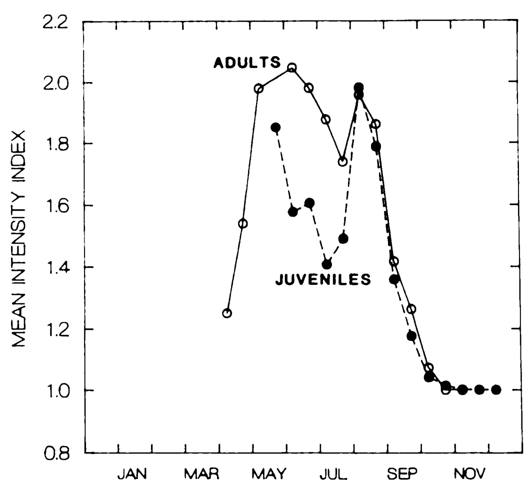

FIGURE 3. Mean intensity of ticks (*Haemaphysalis leporispalustris*) on 3,852 adult and 3,844 juvenile snowshoe hares at semi-monthly intervals during 1963 to 1976. The minimum number of adult or juvenile hares examined in any plotted semi-monthly interval was 20. See text for description of intensity index.

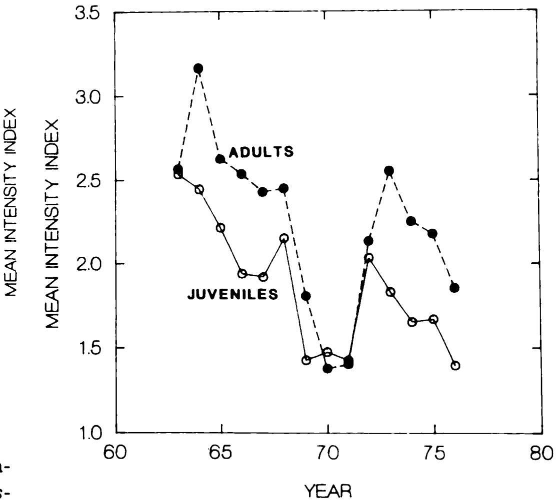

FIGURE 4. Mean intensity of ticks (*Haemaphysalis leporispalustris*) on 2,336 adult and 2,405 juvenile snowshoe during June to August of 1963 through 1976. The minimum number of adult or juvenile hares examined in any plotted June to August period was 12. See text for description of intensity index.

The rapidity with which young hares became infested is shown in Figure 2. Mean prevalence was 61% at age 11 to 20 days, 82% at 21 to 30 days, and 97% at 61 to 70 days.

Intensity

Seasonal changes in intensity of infestation (Fig. 3) paralleled those in prevalence (Fig. 1). Intensity indices for both adult and juvenile hares exhibited a bimodal pattern caused by a midsummer decline (Fig. 3). Tick numbers during July were lower than during 16 May to 30 June and 1 to 15 August (adult hares, $t = 6.37$, df = 2,541, $P \leq 0.01$; juveniles, $t = 8.74$, df = 2,092, $P \leq 0.01$).

Between-year trends in mean intensity were marked and broadly similar among adult and juvenile hares (Fig. 4). Intensities were lowest during 1969 to 1971, when the snowshoe population was at or near peak densities (Fig. 5).

Tick intensities on adult hares tended to be greater among males than females in the pooled data for 1963 to 1976 ($t = 7.72$, df = 2,451, $P \leq 0.001$). This difference (Fig. 6) was significant ($P \leq 0.03$) in five

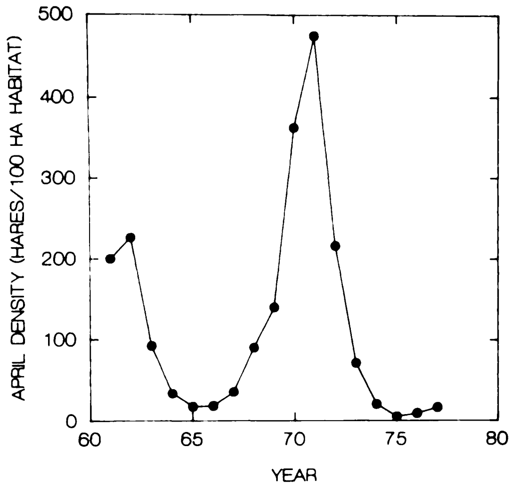

FIGURE 5. Snowshoe hare densities on study areas near Rochester, Alberta (from Keith and Windberg, 1978; L. B. Keith, unpubl.).

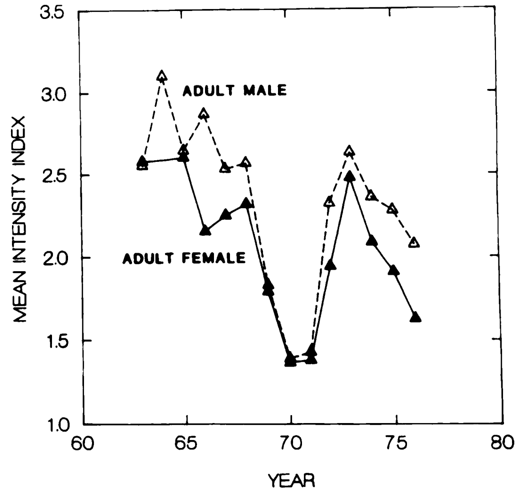

FIGURE 6. Mean intensity of ticks (*Haemaphysalis leporispalustris*) on 1,269 adult male and 1,065 adult female snowshoe hares during June to August of 1963 through 1976. The minimum number of male or female hares examined in any plotted June to August period was 10. See text for description of intensity index.

of the 13 yr (1966, 1968, 1972, 1975, 1976), and approached significance ($P \leq 0.15$) in two others (1967, 1974). During the three consecutive years, 1969 to 1971, when snowshoe hare densities were highest and tick intensities lowest, there was no sex-specific difference ($P \geq 0.45$).

In contrast, with adult hares, tick intensities on juveniles (Fig. 7) were, overall, not different between the sexes ($t = 0.835$, df = 2,235, $P = 0.40$). In only 1 yr (1976) was mean intensity significantly greater among males ($P = 0.04$); during two other years (1968 and 1974) this difference approached significance ($P = 0.09$). Note that these were also years when the sex-specific difference occurred among adults.

Hare survival in relation to tick infestation

To explore possible effects of ticks on hare survival, recapture rates (after August) of marked adults and juveniles were compared with their earlier (June to August) tick-intensity ratings (Table 1). Such recapture rates (survival indices) did not differ significantly among the intensity ratings for either adults (Chi-square = 5.36, df = 4, $P = 0.25$) or juveniles (Chi-square = 3.78, df = 4, $P = 0.43$). Nor did recapture rates tend to decline with increasing intensity. We thus conclude that hare survival was unaffected by levels of tick infestation.

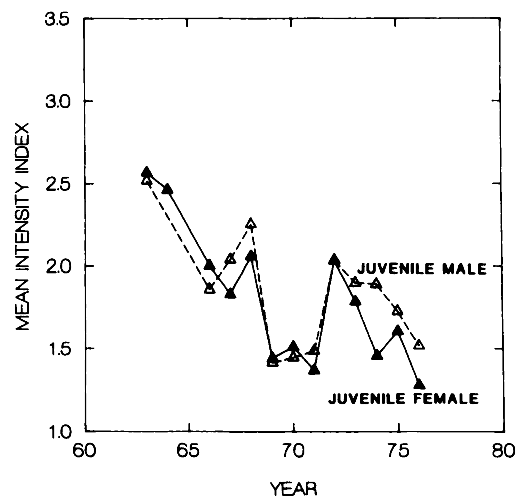

FIGURE 7. Mean intensity of ticks (*Haemaphysalis leporispalustris*) on 1,213 juvenile male and 1,166 juvenile female snowshoe hares during June to August of 1963 through 1976. The minimum number of male or female hares examined in any plotted June to August period was 13. See text for description of intensity index.

TABLE 1. Survival of snowshoe hares in relation to intensities of tick infestation during June to August 1963 to 1976. Survival indexed by recapture rates after August of hares trapped and released during June to August.

Hare age class		Rating of tick numbers on hares during June to August[a]					P[b]
		None	Very few	Few	Moderate	Heavy or very heavy	
Adult	Number of hares released during June to August	50	659	626	370	96	
	% Recaptured after August	28.0	25.0	26.5	20.3	25.0	0.25
Juvenile	Number of hares released during June to August	179	973	646	264	98	
	% Recaptured after August	14.7	13.9	15.2	16.7	9.2	0.43

[a] See text for explanation of rating of tick intensities.
[b] Probability that recapture rates differ (Chi-square tests) among the five tick-intensity ratings within adult and juvenile age classes.

Hare reproduction in relation to tick infestation

We compared hare ovulation rates (mean numbers of corpora lutea) and litter sizes (mean numbers of viable embryos in utero) among the different tick-intensity ratings (Table 2). First and later litters of the breeding season were segregated in this analysis because the former are consistently smaller (Cary and Keith, 1979). During first-litter gestation (data from late March to early May) heavy or very heavy infestations of ticks were rare on adult females, and are thus absent from Table 2. Mean numbers of corpora lutea differed significantly among the four remaining tick-intensity ratings, but did not decline with increasing intensity. Mean numbers of viable embryos in first-litters did not differ nor vary with tick intensity.

Information from later litters, when some adult females were heavily infested with ticks, suggests that both ovulation rates and litter sizes may thereby have been affected (Table 2). Differences among the five tick-intensity ratings had P values of 0.14 and 0.10 for mean ovulation rates and litter sizes, respectively. These relatively low probabilities were primarily caused by smaller means among females with heavy

TABLE 2. Mean ovulation rates and litter sizes of snowshoe hares, as indexed by numbers of corpora lutea and viable embryos in utero, in relation to intensities of tick infestation during April to August, 1963 to 1976. Number of hares examined is shown in parentheses.

Litter of breeding season	Ovulation-rate and litter-size indices	Rating of tick numbers on hares during April to August[a]					P[b]
		None	Very few	Few	Moderate	Heavy or very heavy	
First	Mean number of corpora lutea	3.01 (34)[c]	2.65 (31)	3.10 (29)	2.69 (16)		0.02
	Mean number of viable embryos	2.88 (33)	2.59 (29)	3.00 (29)	2.60 (15)		0.26
	% Prenatal loss of ova or embryos	4.3	2.3	3.2	3.3		
Later	Mean number of corpora lutea	5.31 (15)	5.13 (98)	5.29 (169)	5.46 (63)	4.47 (15)	0.14
	Mean number of viable embryos	5.15 (13)	4.85 (85)	4.95 (164)	4.86 (56)	3.87 (15)	0.10
	% Prenatal loss of ova or embryos	3.0	5.5	8.2	11.0	13.4	

[a] See text for explanation of ratings of tick intensities.
[b] Probability that means differ (ANOVA tests) among the 4 to 5 tick-intensity ratings within first and later litters.
[c] Number of hares examined.

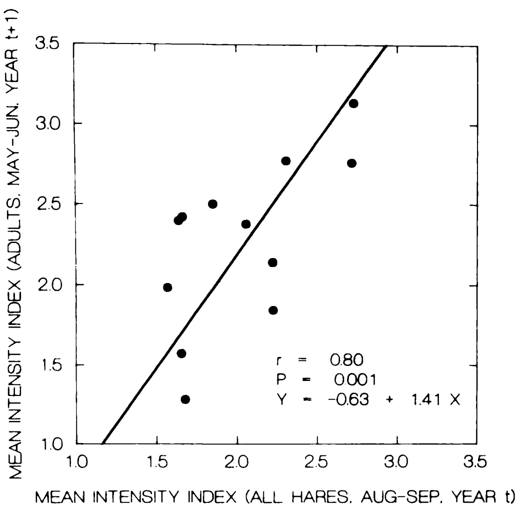

FIGURE 8. Relationship between tick (*Haemaphysalis leporispalustris*) intensities on 1,417 adult snowshoe hares during May–June and on 1,569 adult and juvenile hares during August–September of the previous year. The minimum number of hares examined in any May–June or August–September period was seven. See text for description of intensity index.

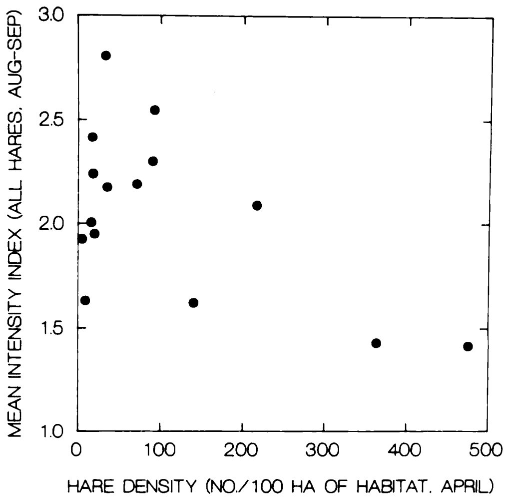

FIGURE 9. Relationship between tick (*Haemaphysalis leporispalustris*) intensities on 1,569 adult snowshoe hares during August–September and densities during the previous April. The minimum number of hares examined in any August–September period was seven. See text for description of intensity index.

and/or very heavy infestations. Of perhaps greater relevance was the tendency for prenatal losses (pre- or postimplantation), as measured by the difference between numbers of corpora lutea and viable embryos, to increase steadily from 3% to 13% with increasing intensities of tick infestation.

DISCUSSION

Seasonal intensities

The seasonal pattern of change in tick intensity at Rochester (Fig. 3) parallelled that recorded earlier among snowshoe hares in Minnesota (Green et al., 1943) and cottontail rabbits (*Sylvilagus floridanus*) in Illinois (Mohr and Lord, 1950). In each case, ticks were absent or rare during December to February, and tended to attain peak numbers during both May–June and August–September. The same dual peaks in intensity were also noted among snowshoes in Nova Scotia (Campbell et al., 1980). As with the previous studies, this probably reflected a heavy infestation by mainly adult ticks in spring, their deaths after egg laying and a subsequent increase in larvae by late summer.

Annual intensities

Green et al. (1943) proposed that tick intensities in spring, a reflection of tick population size, depend importantly upon tick intensities the previous fall. This alleged relationship was verified by the significant correlation in our Rochester data (Fig. 8) between mean intensity during May–June versus the previous August–September.

Green et al. (1943) further proposed that tick intensities in fall depend on hare numbers the previous spring—intensities on their Minnesota study area rose markedly when hare densities exceeded a threshold of about 1/ha. Our data, on the other hand, yielded no evidence that tick and snowshoe hare populations were so related. Tick-intensity indices ranged from high to low in years of lowest hare density, and were lowest during August–September in three of the 4 yr when April hare densities were highest (Fig. 9). The resulting correlation was both negative and significant (r =

-0.58, $P < 0.03$). We tested for possible delayed-density dependence by comparing tick-intensity ratings with both spring and fall densities of hares 1 to 5 yr earlier: none of the correlations was significant ($r \leq 0.31$, $P \geq 0.27$).

Sex-specific intensities

Campbell et al. (1980) found 1.4 times more *H. leporispalustris* on male snowshoe hares than on females, and suggested that the males' larger home ranges and greater mobility may have increased rates of contact with ticks. This sex-specific difference in intensity was likewise observed at Rochester, but only among adult hares and not in those years (1969 to 1971) when hare population densities were highest (Fig. 5). These observations are compatible with the idea that sex-, age- and density-related differences in home-range size (reviewed by Keith, 1990) may affect tick intensities. For example: (1) among adult-size snowshoe hares, annual home ranges of males average about 30% larger than those of females, and female home ranges are much reduced during late pregnancy; (2) home ranges of juveniles from birth to age 1 to 2 mo are apparently only one-half the size of adult home ranges; and (3) home-range size varies inversely with population density, reductions of 60% in mean monthly home ranges have accompanied four-fold increases in density.

Immune response

In Minnesota, mean numbers of ticks per hare during August–September varied from approximately 1,000 to 5,000 over a 10-yr period (Green et al., 1943). On the same study area during the same years, cottontail rabbits averaged only one-fourth as many ticks. McGowan (1985) showed experimentally that domestic rabbits (*Oryctolgus cuniculus*), and probably cottontails (McGowan et al., 1982), have an immune mechanism which reduces tick burdens, whereas the snowshoe hare does not. This, he speculated, may result in a gradual accumulation of ticks to the high levels of infestation commonly observed on snowshoes.

We sought evidence of an immune response in the wild by comparing tick-intensity indices of adult hares age 1, 2, and ≥3 yr during August to September, 1971 to 1974. These were years of population decline when adults ≥2-yr-old comprised a sufficiently high proportion of our trapped sample to make such a comparison possible. Mean-intensity indices did not differ (ANOVA, $P > 0.22$) among the three adult age classes during 1971 to 1973, but approached statistical significance in 1974 ($P = 0.06$). There was no consistent relationship between adult age and mean-intensity indices. Because adult survival was also unrelated to intensity of infestation (Table 1), the failure of mean intensity to decrease with age (i.e., with increased exposure) suggests to us that little if any lasting immunity is developed.

Lyme disease

Public and scientific interest in Lyme disease, and knowledge of its etiology, increased during the past decade. The spirochete (*Borrelia burgdorferi*) causing Lyme disease has been isolated from *H. leporispalustris* (Anderson and Magnarelli, 1984; Lane and Burgdorfer, 1988); and both the spirochete and *Borrelia* sp. antibodies have been found in many mammals including cottontails (*S. floridanus* and *S. audubonii*) and jack rabbits (*Lepus californicus*) (Burgess and Windberg, 1989; Lane and Regnery, 1989). The geographic range of this disease organism is clearly much larger than appreciated initially. To our knowledge, nothing has been reported on the occurrence of spirochetes or antibodies in snowshoe hares. We suspect, however, that the strongly-cyclic hare populations of Canada and Alaska, with their high prevalences and intensities of *H. leporispalustris*, may well constitute major reservoirs of *Borrelia* sp. Although *H. leporispalustris* rarely engorges on humans, there are perhaps other potential vectors of *Borrelia* sp. that do so. The

American dog tick (*Dermacentor variabilis*), for example, is homophilic and found on snowshoe hares from southern Manitoba eastward. This species has been implicated as a vector of the spirochete (Anderson et al., 1985), but may not be competent (Mather and Mather, 1990).

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