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**Abstract**

We studied snowshoe hare (*Lepus americanus*) populations near Fredericton, New Brunswick from June 1967 to February 1971. Total population numbers on a 180-ha study area decreased from an estimated 294 hares in September 1967, a year of high population density, through three years of declining numbers to 29 hares in October 1970. Annual adult survival rates varied from 0.17 to 0.31 throughout the study, and monthly juvenile survival increased from 0.75 in the first year of study to 0.84 in the two following years. Conceptions of all three litters were closely synchronized. Samples from Prince Edward Island, southwestern Nova Scotia and Blackville, N.B., 120 km north of Fredericton, were similarly synchronized. No fourth litters were detected in any areas sampled. First litters were significantly smaller than later litters in all areas. We found some differences among years and areas in litter size and pregnancy rates; recruitment rates differed somewhat among years and areas. Total mean annual recruitment was 5.46 per adult female. Yearling females contributed fewer young than older adults through lower pregnancy and ovulation rates, and yearling females may have lost entire litters through resorption more often than older adults. We have compared these population parameters to findings in other areas of the snowshoe hare's range, and the differences are discussed.

**Résumé**

Les populations de lièvre d'Amérique (*Lepus americanus*) de la région de Fredericton (Nouveau-Brunswick) ont fait l'objet d'une étude entre juin 1967 et février 1971. Dans l'aire choisie de 180 hectares, l'effectif en est passé d'un nombre estimatif de 294 lièvres en septembre 1967, année où fut enregistrée une forte densité démographique, à 29 en octobre 1970, après trois années consécutives de déclin. Le taux annuel de survie chez les adultes a varié entre 0.17 et 0.31 au cours de l'étude alors que le taux mensuel en passait chez les jeunes lièvres de 0.75 la première année à 0.84 les deux années suivantes. La conception de chacune des trois portées se fit à peu près à la même date. Semblable synchronisme est apparu chez les échantillons de l'Île-du-Prince-Édouard, du sud-ouest de la Nouvelle-Écosse et de Blackville (Nouveau-Brunswick), à 120 kilomètres au nord de Fredericton. On n'a décelé de quatrième portée dans aucune des aires échantillonnées. Partout la première portée fut significativement plus petite que les suivantes. Selon l'année et l'aire, on enregistra des différences d'effectif des portées ainsi que des taux de gestation et de reproduction. Le taux annuel moyen de reproduction était de 5.46 par femelle adulte. L'apport en levrauts des femelles d'un an était, du fait d'un taux de gestion et d'ovulation plus faible, moindre que celui de leurs ainées. Il se peut qu'il soit arrivé plus souvent aux femelles d'un an de perdre une portée entière par résorption. Comparaison s'est faite de ces paramètres démographiques à ceux d'autres régions comprises dans l'aire de distribution du lièvre d'Amérique et l'analyse des différences observées.

# Introduction

The snowshoe hare (*Lepus americanus*) is common in most boreal forest areas of North America. The species is cyclic in abundance, becoming very numerous about every 10 years. A research group under L. B. Keith has been intensively studying phenomena related to this cyclic abundance in Alberta since 1961, and has shown that the combined changes in length of breeding season, pregnancy rate and litter size, as well as adult and juvenile survival, produced the dramatic fluctuations in snowshoe hare population numbers witnessed in the aspen forest of central Alberta.

In the Maritime Provinces the snowshoe hare is also common, but has been relatively little studied. Together with white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*), hares are abundant browsing mammals in the forests of the area, where the economy is largely based on woodland industries. A Canadian Wildlife Service (CWS) study was initiated at the request of the Canada Department of Forestry and Rural Development in June 1967 as part of studies of mammal–forest ecology. The work, to investigate the population status and dynamics of the snowshoe hare in the Maritimes, continued until February 1971.

Our investigations of snowshoe hare population dynamics were designed to use many of the same techniques as the Alberta study, and we present the results in a similar way to yield directly comparable information.



# The study area

Field work was conducted at the Acadia Forest Experiment Station about 24 km east of Fredericton, N.B. The station, 91 km$^2$ in area, lies within the Maritime Lowlands Ecoregion, a part of the Red Spruce–Hemlock–Pine Zone described by Loucks (1962). Principal coniferous tree species are red spruce (*Picea rubens*), black spruce (*P. mariana*), balsam fir (*Abies balsamea*) and larch (*Larix laricina*), with white cedar (*Thuja occidentalis*), white pine (*Pinus strobus*) and eastern hemlock (*Tsuga canadensis*) of lesser importance. Common deciduous trees are sugar maple (*Acer saccharum*), red maple (*A. rubrum*), white birch (*Betula papyrifera*), yellow birch (*B. alleghaniensis*) and trembling aspen (*Populus tremuloides*). Soils are moderately well drained loams. Stream valleys, lower slopes, and poorly drained uplands support coniferous growth. Stands of birches and maples are found on upper slopes. Other areas support stands of mixed conifers and deciduous trees. Wildfire burned much of the Acadia station forests prior to 1930. Currently much of this burned area supports open, patchy forest stands. Logging, mostly during the past 10 years, has resulted in stands of seedlings and saplings (Telfer 1970).

A 180-ha study area, judged representative of the forests of central New Brunswick (E. S. Telfer, pers. comm.) was selected for the purpose of hare population studies. This area is in the centre of the Acadia station, and is bounded on three sides by gravel roads and on the fourth by forest. Access lines, 201 m apart, connecting permanent forestry sampling plots, were used as grid lines, with reference points for trapping and other purposes spaced every 101 m along each line.

We collected hares for post-mortem examination within a 40 km radius of Fredericton. For comparison, collections were also made 120 km north of Fredericton around the towns of Blackville and Upper Blackville on the Southwest Mirimachi River, on Prince Edward Island, and in southwestern Nova Scotia.

Both the Fredericton and Blackville sampling areas are within Loucks' (1962) Maritime Lowlands Ecoregion. Fredericton is low lying (<150 m altitude) and Blackville more upland (150–300 m) with a somewhat more severe climate. The sampling area of southwestern Nova Scotia (inland Digby and Yarmouth counties) is located in Loucks' (1962) Clyde River–Halifax Ecoregion, also part of the Red Spruce–Hemlock–Pine Zone, but characterized by more shallow, sandy soils, with red oak as the common deciduous associate. Climate is less severe than in either New Brunswick area. The sample area on Prince Edward Island is located mainly in Loucks' Magaguadavic–Hillsborough Ecoregion, part of the Sugar Maple–Hemlock–Pine Zone. There, soils are light-textured podsols, and tolerant hardwoods are found on a wide range of sites. Climate is more moderate than in New Brunswick, but more severe than in southwestern Nova Scotia.

# Methods

Hares were live-trapped (Keith, Meslow, and Rongstad 1968) using unbaited, single-door National Live Traps (23 x 23 x 61 cm) at the Acadia station study area during the following periods: September–October and December 1967; April–May, June–July, August, and September–October 1968; April–May, July, August, and October 1969; April–May, July, and October 1970. Trapping periods averaged 11 days (range 8–18); those in summer were generally 8–10 days, and those in early spring and autumn were 16–18 days in length.

Live trapping was done in areas with sufficient ground cover and runways, fresh clippings, and fecal pellets. These locations were concentrated in and around softwood bogs, and softwood and mixedwood stands with ground cover. We did not trap intensively in the several hardwood stands on the study area because they lacked hare *sign*, especially hare tracks in snow. To maintain randomness in both captures and recaptures (Keith and Meslow 1968), traps were continually relocated. Runways through dense brushy cover were selected for trapping. The cover was often augmented with sticks to provide a funnel leading to the trap entrance.

We marked hares with monel metal fingerling tags placed behind the intercapitular ligament in the interdigital webs of each hind foot. Hares older than about one month were also ear tattooed. During April–May trap periods, all adult females were implanted subcutaneously with a gelatinous capsule of radio-active calcium, $Ca^{45}$ (Rongstad 1965). Young born of the implanted females during the ensuing season were detectably radioactive. We clipped two toes from the front feet of each newly captured juvenile and analyzed them to obtain a ratio of radioactive to non-radioactive young.

Hare populations on the study area were estimated using the Petersen–Lincoln Index. Keith and Meslow (1968) demonstrated that captures by trapping were generally random when trap sites were continually changed and when marked/unmarked ratios were taken at a time later than the marking period. We made estimates of autumn 1967, and spring, summer, and autumn 1968–70 hare populations, using marked/unmarked ratios obtained from live-trapping data. Estimates were made of spring adult numbers in 1968 and 1969 using the ratio of radioactive/non-radioactive juveniles, assuming a 50:50 adult sex ratio. In 1970, too few young were trapped to allow confidence in the latter method.

From 1967 to 1970 snowshoe hares were collected by shooting in fields and on roadsides within a 40 km radius of Fredericton from March to August, and in the vicinity of Blackville, N.B. from June to August. Samples were also obtained from Prince Edward Island (1968 and 1969) and southwestern Nova Scotia (1968 to 1970). All specimens were necropsied and examined for reproductive data.

We examined embryos for viability and determined their age according to data given by L. B. Keith (pers. comm.), Joseph Dell (unpubl.), and Bookhout (1964). The sex of embryos 25 days or more post-conception was determined by internal examination of gonads. Testes were sectioned, stained, and examined for signs of spermatogenic activity. Ovaries were hand-sectioned after fixation, and *corpora lutea* counted. Eye lenses were removed within several hours of death and fixed in 10% formalin. We then dried and weighed them for age determination according to the technique described by Friend (1965). Ages were determined using age/lens-weight data presented by Keith *et. al.* (1968).



# Results

**Table 1**
Snowshoe hare population estimates on 180-ha study area at Acadia Experiment Station, New Brunswick

| Spring* | | | Summer* | | | Autumn* | | |
|---|---|---|---|---|---|---|---|---|
| Mean date | No. est. | Basis† | Mean date | No. est. | Basis† | Mean date | No. est. | Basis† |
| Spring 1967 | 385 | A | Summer 1967 | 260 | A | Sept. 28 1967 | 294 (106–684) | B |
| April 30 1968 | 110 (66–170) | B | July 7 1968 | 90 (29–230) | B | Sept. 23 1968 | 93 (33–215) | B |
| | 115 (69–178) | C | Aug. 7 1968 | 64 (14–236) | B | | | |
| | $\bar{x}$ 112 | | | $\bar{x}$ 77 | | | | |
| May 8 1969 | 58 (16–173) | B | July 31 1969 | 44 (17–95) | B | Oct. 16 1969 | 70 (31–136) | B |
| | 103 (44–215) | C | | | | | | |
| | $\bar{x}$ 80 | | | | | | | |
| May 7 1970 | 57 (16–168) | B | July 26 1970 | 49 ( 8–276) | B | Oct. 16 1970 | 29 ( 9–73) | B |

*Spring and summer estimates include young of previous year, while autumn estimates also include young of the same year. Confidence limits are at the 95% level, based on Overton and Davis (1969).
†Estimated numbers based on: A. Extrapolation of the average 1968–70 spring–summer–autumn variation in abundance. B. Petersen–Lincoln Index estimate based on recapture data. Recapture period was the next trapping period, except in the fall estimate, where periods were divided into two equal parts — the trap period and the recapture period. C. Petersen–Lincoln Index estimates based on recapture of radio-isotope tagged juveniles (Rongstad 1965).

## 1. Population indices

Although no quantitative data are available prior to 1967, subjective estimates by experienced personnel indicated that hares were much more numerous during 1967 than the several previous years. Our data show a distinct decline from the autumn of 1967 to 1970 (Table 1). Limited field work during the winter of 1970–71 indicated that the hare population of 1971 had not increased from the level of 1970, and may have declined further (Wood, unpubl. data; C. Bursey, pers. comm.).

Captures per 100 trap-nights (Table 2) also indicate a declining population from 1967 to 1970. The apparent discrepancy between the autumns of 1967 and 1968, when trapping was done largely in September, and the autumns of 1969 and 1970, when trapping was done largely in October, may be partly explained by the greater ease of trapping, and presumably the greater vulnerability to trapping, in October, after the leaves had fallen and the herbaceous vegetation died back, than in September. It is possible, then, that autumn trap success would show an even greater decline from 1967 to 1970 had autumn trapping been done in the same month in all years.

**Table 2**
Live capture success in New Brunswick snowshoe hares, 1967–70. Figures in parentheses are total number of trap-nights in period

| | Captures/100 trap-nights | | |
|---|---|---|---|
| Year | Spring | Summer | Autumn |
| 1967 | — | — | 10.8 ( 860) |
| 1968 | 8.6 ( 978) | 5.6 (2484) | 4.3 (1656) |
| 1969 | 4.4 (1196) | 3.4 (1632) | 7.9 (1012) |
| 1970 | 3.4 (1650) | 1.0 (1009) | 3.9 ( 920) |

## 2. Movements

Data on distances moved from points of capture indicate that the hare is relatively sedentary in nature (Seton 1929, Grange 1932, Adams 1959, Bider 1961, O'Farrel 1965, Meslow and Keith 1968). Our findings were similar to those of the above authors: in this study 94% of adult and 91% of juvenile recaptures during the spring–autumn trapping season were within 0.40 km of the initial point of capture; and 88% of adults and 82% of juveniles recaptured in spring or summer were less than 0.40 km from where they had been marked in a previous year.

Meslow and Keith (1968) found that juveniles moved significantly shorter distances than adults during the first three months after marking. In the present study, juvenile movements

did not differ significantly from those of adults in either the summer–autumn or winter periods. Mean over-winter distances moved by animals marked as juveniles (mean = 187 m, n = 92) were significantly ($P < 0.05$) greater than juvenile summer–autumn movements (mean = 114 m, n = 28) (t = 2.62, d.f. = 60). Adult hares did not show this difference.

Adult males moved significantly ($P < 0.05$) greater distances (mean = 165 m, n = 101) than adult females (mean = 105 m, n = 69) during summer (t = 2.78, d.f. = 85), but no such difference was displayed in winter. Similarly, juvenile females moved significantly ($P < 0.05$) greater distances (mean = 139 m, n = 58) than juvenile males (mean = 77 m, n = 34) during summer (t = 2.05, d.f. = 46), but differences were not significant in winter.

## 3. Survival

Adams (1959) and Meslow and Keith (1968) showed that by October sub-adult mortality was similar to that in the adult cohort. Green and Evans (1940*b*) found proportions of sub-adults to be similar between December and March. Proportions of yearlings in spring were lower than proportions of sub-adults in autumn for 3 of 4 years in this study (Table 3), indicating that differential mortality in sub-adults persisted over winter in all winters except 1970–71. Rates of capture in another year of autumn-marked animals also showed this difference. Only 15% (n = 115) of autumn-marked juveniles were recaptured another year, while 36% of autumn-marked adults were recaptured another year.

We calculated average annual adult survival rates, spring to spring, by the following formula:

$$\frac{\text{spring population year 2 x percent adults year 2}}{\text{spring population year 1}}$$

**Table 3**
Percentages of sub-adult and yearling hares in population.*
Sample sizes in parentheses

| Year | Autumn (Sept.–Oct.) % sub-adults | Spring† (March–May) % yearlings | Summer† (June–Aug.) % yearlings | Mean |
|---|---|---|---|---|
| 1967–68 | 63 (84) | 43 (76) | 53 (38) | 54 (198) |
| 1968–69 | 75 (48) | 57 (80) | 50 (64) | 59 (192) |
| 1969–70 | 63 (60) | 59 (77) | 49 (57) | 57 (194) |
| 1970–71 | 48 (27) | 56 (43)‡ | | |

*Autumn age ratios based on live-trapped sample aged by condition of external genitalia. Sub-adults considered fully active and equally as vulnerable to trapping as adults.
†Spring and summer age ratios based on shot samples, aged by eye-lens weight technique as described in Meslow and Keith (1968).
‡Spring 1971 age ratio based on sample snared in January and February, 1971, aged by combination of external genitalia and lens weight technique.

**Table 4**
Survival rates of juvenile snowshoe hares

| Year | (A) Est. births* & mean date | (B) Pop'n. est. next spring (Table 1) | (C) % yearlings next spring (Table 3) | (D) Est. young alive next spring (B) x (C) | Survival rate to next spring (D)/(A) | Mean monthly survival rate |
|---|---|---|---|---|---|---|
| 1967–68 | 1129 | 112 | 43 | 48.2 | .0426 (334)† | 0.75 |
| 1968–69 | 304 (June 10) | 80 | 57 | 45.6 | .1500 (332) | .84 |
| 1969–70 | 232 (June 4) | 57 | 59 | 33.6 | .1448 (337) | .84 |
| 1970–71 | 146 (June 17) | | 56 | | | |

*Obtained by applying recruitment rate (Table 8) to 50% of adult population estimate. Spring sex ratios not significantly different from 50:50 (Table 5). Recruitment rate has been corrected for female mortality from mean date of census to birth of final litter.
†Days from mean date of birth to mean date of census following spring. 1967–68 figure based on average of 1968–69 and 1969–70.

Survival rates for 1967–68, 1968–69 and 1969–70 were 0.17, 0.31, and 0.29 respectively. These rates compare favourably with the 0.13–0.28 rates which Meslow and Keith (1968) found in three years of hare population decline in Alberta, and 0.22 found in a declining Montana population (Adams 1959). They are somewhat lower than the 0.28–0.36 survival rates documented in four consecutive years of hare population decline in Minnesota (Green and Evans 1940*b*).

Juvenile survival rates (Table 4) were computed, using the method described by Meslow and Keith (1968), and indicated a pattern like that displayed in Alberta: a distinct increase in monthly juvenile survival after the first winter of population decline (1967–68 in this case). Data from this study are most nearly equal to the mean monthly survival rates of Minnesota hares during five years of decline—0.85, 0.87, 0.83, 0.79, and 0.75 (Green and Evans 1940*c*), and higher in most years than comparable data recorded in Alberta—0.69, 0.70 and 0.78 (Meslow and Keith 1968), and Montana—0.76 (Adams 1959).

## 4. Sex ratios

During 1967–70 *in utero* litters were sexed by examination of gonads. After some experimentation, we concluded that only embryos older than 25 days could be sexed reliably. New Brunswick and Nova Scotia *in utero* litters showed a preponderance of males in all years, but in no year did the sex ratio differ significantly from 1:1 (New Brunswick, 1967–70, 53% males in 377 embryos; Nova Scotia, 1968–70, 65% males in 37 embryos). Prince Edward Island litters showed a slight preponderance (not significant) of females (52% of 50 embryos). These findings agree with those of Meslow and Keith (1968) and earlier workers in showing little evidence for *in utero* differential mortality in hares.

Juvenile hares live-trapped in summer and autumn in New Brunswick showed a slight preponderance of females, but this difference was not significant (45% males in 246 captures). Juveniles shot in New Brunswick had a significant preponderance of females (38% males in 100 shot). As discussed below, we believe the live-trapped sample to be most representative of the New Brunswick population, as shot samples seem to favour collection of females.

Adult male hares showed a greater susceptibility to capture during the breeding season, as reflected in the March–May preponderance of males in the live-trapped sample (Table 5). Bider (1961) found that males have larger home ranges than females, and Meslow and Keith (1968) suggested that this may make males more vulnerable to trapping.

**Table 5**
Sex ratios of adult New Brunswick snowshoe hares. Sample sizes in parentheses

| Capture method & season | % males 1967 | 1968 | 1969 | 1970 | Total |
|---|---|---|---|---|---|
| *Shot* | | | | | |
| March–May | | 40* (129) | 44 (145) | 38* (101) | 41* (375) |
| June–Aug. | 19* (92) | 18* (95) | 25* (96) | 24* (105) | 21* (388) |
| Sept.–Oct. | | | | (1) | (1) |
| Total | 19* (92) | 31* (224) | 36* (241) | 31* (207) | 30* (764) |
| *Live-trapped* | | | | | |
| March–May | | 59 (65) | 61 (38) | 57 (40) | 59* (143) |
| June–Aug. | | 46 (78) | 57 (14) | 67 (6) | 49 (98) |
| Sept.–Oct. | 49 (43) | 67 (12) | 50 (22) | 86 (14) | 57 (91) |
| Total | 49 (43) | 53 (155) | 57 (74) | 65* (60) | 55* (332) |
| *Both methods* | | | | | |
| March–May | | 46 (194) | 48 (183) | 43 (141) | 46 (518) |
| June–Aug. | 19* (92) | 31* (173) | 29* (110) | 26* (111) | 27* (486) |
| Sept.–Oct. | 49 (43) | 67 (12) | 50 (22) | 87* (15) | 58 (92) |
| Total | 28* (135) | 40* (379) | 41* (315) | 39* (267) | 38* (1096) |

*Significantly different from 1:1 at 95% level.

Sex ratios of adult hares collected in New Brunswick by shooting showed a preponderance of females, particularly from June to August. However, early in the spring, when hares were shot exclusively in fields where they gathered to eat the first green shoots, the sex ratio was about 1:1. In 1969 all hares collected up to May 15 were taken in fields and the proportion was 47% males (n = 135). After that date, when hares began appearing in large numbers on roadsides to eat soil and sand, the proportion of males dropped to 23% (n = 114). This indicated that adult female hares were more strongly attracted to gravel and dirt roads to consume soil or sand. In 1969, sand varying in amounts from a trace to 41 g was found in 46% of the female, but only 27% of male stomachs examined. This attraction to roadsides in summer distorts the sex ratios of animals collected by shooting at that time.

Newson and deVos (1964) also took a significantly ($P < 0.05$) larger proportion of females when hares were shot in the spring and summer on roads and in the fields, but ratios did not

differ from equality when hares were snared during the same period.

Because of an apparently greater susceptibility of males to capture in the breeding season, and the demonstrated preponderance of females on roads after mid-May, the sex ratio data in Table 5 must be viewed with caution. The sex ratios of the sample live-trapped in autumn and that shot in early spring are probably the least biased. Since neither differs significantly from equality, we concluded the adult sex ratio was 1:1.

## 5. Reproduction

Mean data of first litter conception (Fig. 1) was synchronized in each year and area. This agrees with findings from Ontario (MacLulich 1937, and Newson 1964), Michigan (Bookhout 1965), and Alberta (Meslow and Keith 1968), but differs from Montana, where Adams (1959) found dates of initial conception ranged over 3–4 weeks. Conceptions of later litters were also grouped, with the average interval between conception peaks (35.5 days) very closely approximating the mean 37-day gestation period found by Severaid (1942) for captive hares in Maine, and the 34.4-day interval found between conception peaks in Alberta (Meslow and Keith 1968). MacLulich (1937), Severaid (1945), Newson (1964), and Meslow and Keith (1968) all found distinct grouping in later litters, and Bookhout's (1965) data suggested such grouping.

We found little variation among years in the timing of breeding onset for any one area in this study. Samples from Fredericton, where the most complete collection was made, varied only 5 days (April 5–10) in the 4 years studied. Data on the onset of breeding from Blackville, while less complete and based on second-litter groupings, showed only 9 days' variation (April 13–22). Similarly, Nova Scotia showed little variation between years (April 1–6), while samples from Prince Edward Island were too small for valid conclusions.

Meslow and Keith (1971) found the mean date of first-litter conception in Alberta varied 21 days (March 25–April 15) during 8 years, but that breeding was very closely synchronized in any one year. A correlation was found in Alberta between degree of cloud cover in January to March and date of initiation in breeding. In Fredericton, total hours of sunshine from January to March (measured on a Campbell-Stokes sunshine recorder at the Fredericton Airport) were 349 in 1967, 397 in 1968, 311 in 1969, and 439 in 1970. Little variation among years in onset of breeding was seen in this study at Fredericton (Fig. 1), and no correlation with hours of sunshine is evident.

To ascertain pregnancy rates during the various first, second, and third litter groupings, only animals collected during the middle 20-day period between conception peaks were considered. Only females with visible implantations were considered pregnant. Rates of first-litter pregnancy (Table 6) averaged about 90% for all Fredericton collections and for the 1970 Nova Scotia sample. We found no significant differences between years in Fredericton first-litter rates, thus the mean (0.91) value was used to represent the 1967 first-litter rate. The 1969 first-litter pregnancy rate from Nova Scotia differed significantly from both the 1970 Nova Scotia rate and the mean rate for first-litter pregnancies in Fredericton. The 1969 Prince Edward Island rate also differed significantly from the Fredericton mean.

Despite the fact that we demonstrated evidence of between-year differences in first-litter pregnancies from the same area (1969–1970, Nova Scotia), we believe that mean pregnancy rates from a particular locale offer the best



**Table 6**
Rates of visible pregnancy among necropsied female hares examined during middle 20 days gestation of different litter groups.
Sample sizes in parentheses*

| Location | Year | 1st litter | 2nd litter | 3rd litter |
|---|---|---|---|---|
| Fredericton | 1967 | 0.91 | 0.91 (11) | 0.79 (24) |
| | 1968 | $\bar{x}$0.91 { 0.96 (25) | 0.87 (23) | 0.82 (22) |
| | 1969 | 0.95 (36) | 0.94 (18) | 0.75 (16) |
| | 1970 | 0.80 (20) | 0.70 (23) | 1.00 (18) |
| Blackville | 1967 | 0.91 | 0.92 | Mean rate |
| | 1968 | 0.91 | 0.93 (14) | |
| | 1969 | 0.91 | $\bar{x}$0.92 { 1.00 (21) | 0.86 (7) |
| | 1970 | 0.91 | 0.83 (18) | |
| Nova Scotia | 1968 | 0.71 | Mean rate | Mean rate |
| | 1969 | $\bar{x}$0.71 { 0.55 (11) | | |
| | 1970 | 0.89 (9) | 0.83 (18) | 0.75 (20) |
| P.E.I. | 1968 | 0.71 | Mean rate | 0.71 |
| | 1969 | 0.71 (14) | 0.76 (17) | 0.71 (17) |

*Conclusions concerning size differences of various litter groups were determined by chi-square and are discussed in the text.

estimate for those years when we did not have collections. Thus we used the average of first-litter rates for 1969 and 1970 from Nova Scotia to estimate the 1968 Nova Scotia first-litter pregnancy rate. Similarly, the 1969 first-litter pregnancy rate for Prince Edward Island was used for the missing 1968 data. Since insufficient collecting was done in Blackville during the first-litter pregnancies, the Fredericton mean was used for first-litter pregnancy rate in Blackville. The 1968 and 1970 third-litter mean from Blackville was substituted for the 1969 third-litter rate in Blackville. The 1969 third-litter mean for Prince Edward Island was substituted for the 1968 Prince Edward Island third-litter value.

Rates of pregnancy remained high during the second-litter detection period (Table 6) particularly in the New Brunswick samples, and declined somewhat in the third-litter grouping. The differences between second- and third-litter pregnancy rates were not significant at Fredericton, where sample sizes were complete and adequately large to allow statistical comparison. The only significant differences among years were found in the Fredericton samples: the 1970 second-litter rate was lower and the 1970 third-litter rate was higher than the means of 1967–69. No significant differences in pregnancy rates among areas were found in second- and third-litter groupings.

First litters were consistently smaller than later litters in all years and areas studied (Table 7). No significant differences among areas were found in first-litter size. Significant differences among areas were found in size of later litters, however, with the Blackville mean smaller and the Prince Edward Island and Nova Scotia means larger than the Fredericton mean. Differences among years (Table 7) show considerable variation with no marked pattern evident.

Table 8 shows calculated mean number of litters, mean number of viable embryos per adult female, and recruitment. Despite differences among pregnancy rates and litter sizes described earlier, the annual recruitment rates do not vary greatly. Average recruitment for all years and areas was 5.46. Keith, Rongstad, and Meslow (1966) described increases in recruitment with increasing latitude, and gathered data from many parts of the hare's range to illustrate. Data on recruitment from this study are less than those quoted from Ontario, 6.3 (Newson 1964),

**Table 7**
Mean number of embryos found in adult snowshoe hares* including embryos undergoing resorption in otherwise normally healthy litters.
Numbers of pregnant females examined in parentheses

| Location | Year | 1st litters | Later litters |
|---|---|---|---|
| Fredericton | 1967 | 2.27 | [ 3.26 (47) |
| | 1970 | 2.29 (21) | [ 2.77 (44) |
| | 1969 | $\bar{x}$2.27 { 2.38 (63) | [ 3.10 (40) |
| | 1968 | 2.10 (40) | 2.96 (50) |
| Blackville | 1967 | 2.27 | 2.43 (7) |
| | 1968 | 2.10 (10) | [ 2.95 (19) |
| | 1970 | 2.27 | [ 2.48 (25) |
| | 1969 | 2.27 | [ 2.88 (25) |
| Nova Scotia | 1968 | 2.56 | 3.65 (25) |
| | 1969 | 2.56 (9) | 3.40 (10) |
| | 1970 | 2.57 (7) | 4.00 (6) |
| P.E.I. | 1968 | Mean no. | [ 4.14 (7) |
| | 1969 | 2.64 (14) | [ 3.24 (51) |

*Square brackets join means from same locations which differ significantly at 95% level when compared by t-test. In all cases first litter means were significantly less than later litter means. Other statistical differences are discussed in the text.

**Figure 1**
Conception dates of snowshoe hare litters determined from dissection of wild caught hares. Mean conception dates (dated arrows) were calculated using only pregnancies in which viable embryos could be found. *Dotted* arrows indicate estimated mean conception dates using average periods between peaks determined in other years.

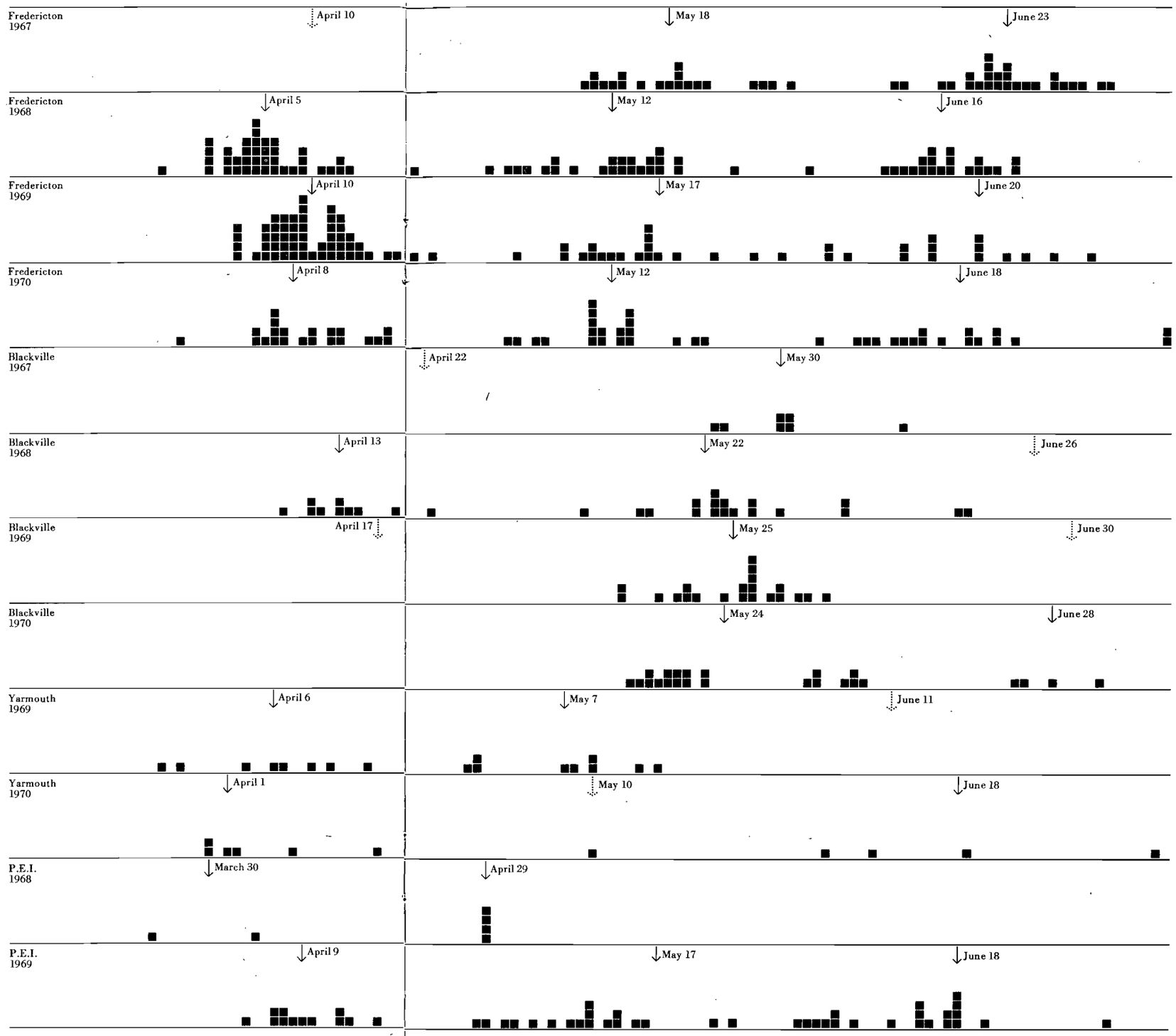

**Table 8**
Estimated number of litters, mean number of viable embryos per adult female, and recruitment, based on litter sizes and pregnancy rates given in Tables 6 & 7

| Location | Year | Mean no. litters | Mean viable embryos/adult female* | Recruitment† |
|---|---|---|---|---|
| Fredericton | 1967 | 2.61 | 7.39 | 5.77 |
| | 1968 | 2.65 | 6.82 | 5.33 |
| | 1969 | 2.64 | 7.28 | 5.69 |
| | 1970 | 2.50 | 6.35 | 4.96 |
| | Mean | 2.60 | 6.96 | 5.44 |
| Blackville | 1967 | 2.69 | 6.21 | 4.85 |
| | 1968 | 2.70 | 6.99 | 5.46 |
| | 1969 | 2.77 | 7.21 | 5.63 |
| | 1970 | 2.60 | 6.08 | 4.75 |
| | Mean | 2.69 | 6.62 | 5.17 |
| Nova Scotia | 1968 | 2.29 | 7.41 | 5.79 |
| | 1969 | 2.13 | 6.58 | 5.14 |
| | 1970 | 2.47 | 8.36 | 6.53 |
| | Mean | 2.30 | 7.45 | 5.82 |
| P.E.I. | 1968 | 2.18 | 7.73 | 6.04 |
| | 1969 | 2.18 | 6.44 | 5.03 |
| | Mean | 2.18 | 7.08 | 5.53 |
| Total mean | | | | 5.46 |

*Adjusted to exclude resorbing embryos in otherwise healthy litters. Resorption rate = 0.029.
†Mean young per adult female alive at spring census, corrected for post-census female mortality (i.e., average annual mortality of 75% used to adjust for female mortality during 3.5-month breeding season).

Michigan, 6.5 (Bookhout 1965), and Minnesota, 6.8 (Green and Evans 1940*c*), all approximately 46°N latitude, similar to Fredericton.

Lens weight/age categories described by Keith *et. al.* (1968) corresponded closely in this study to ages assigned by examining external genitalia. Analysis of reproductive performance of female hares indicated that 2+-year-old hares had a significantly higher second-litter pregnancy rate than yearlings. The difference was not significant in first- or third-litter gestation periods (Table 9). The mean number of embryos per adult female was significantly smaller for yearlings during first-litter pregnancies, but not in second- or third-litter pregnancies. Mean numbers of *corpora lutea* were smaller for yearling females in first- and third-litter pregnancies. No differences between yearling and older females were seen in the occurrence of partial litter resorption, but yearlings may have totally resorbed third litters more often than older adults. The data indicated that yearling females have a somewhat lower production than older adults.

## 6. Population fluctuations

Meslow and Keith (1968) showed that cycles in Alberta hare populations (amplitude 40:1) were a result of combined changes in reproductive parameters and survival. Subsequently, Meslow and Keith (1971) demonstrated a correlation between cold, snowy winters and decreased adult survival, followed by a compensatory increase in litter size.

New Brunswick hare populations fluctuated to a lesser degree (amplitude 10:1). Reproductive parameters in New Brunswick hares were more constant and on a lower scale than in Alberta, where recruitment varied from 5.5 in a year of decline to 15.5 in a year of recovery. Although no period of continued population increase was studied in New Brunswick, recruitment varied less than in Alberta — from 5.8 when the population was high to 5.0 in a year of decline. Litter size, length of breeding season, and pregnancy rate all contributed to the striking change in

**Table 9**
Reproductive performance of yearling and older female New Brunswick hares, 1968–70. Ages determined by lens weights. Sample sizes in parentheses

| | Age class | Prop'n. females visibly pregnant | Mean embryos per female* | Mean *corpora lutea*/ female | Prop'n. embryos resorb.† | Prop'n. litters totally resorbed |
|---|---|---|---|---|---|---|
| 1st litter Det'n. period | 1 yr. | 0.89 (35) | 2.04‡ | 2.10‡ | 0.05 (65) | 0.00 (35) |
| | 2+yrs. | 0.09 (21) | 2.46 | 2.61 | 0.00 (48) | 0.00 (21) |
| 2nd litter Det'n. period | 1 yr. | 0.70 (27)‡ | 2.96 | 3.20 | 0.05 (61) | 0.04 (27) |
| | 2+yrs. | 1.00 (22) | 2.91 | 3.19 | 0.02 (66) | 0.00 (22) |
| 3rd litter Det'n. period | 1 yr. | 0.65 (17) | 2.50 | 3.07‡ | 0.00 (36) | 0.18 (17) |
| | 2+yrs. | 0.75 (20) | 2.86 | 4.44 | 0.08 (47) | 0.05 (20) |

*Adjusted to exclude resorbing embryos in otherwise healthy litters. Resorption rate = 0.029.
†Denotes embryos undergoing resorption in otherwise healthy litters. Total number of embryos in parentheses.
‡Square brackets join data groups which show statistically significant differences using a t-test at the 95% confidence level.

recruitment witnessed in Alberta. New Brunswick populations showed few of these striking changes.

In Alberta, first and later litter sizes increased significantly between years of population decline and years of population increase. In New Brunswick no change was seen in first-litter sizes, and a smaller change than in Alberta was seen in later-litter sizes. Number of litters produced in New Brunswick was fairly constant in all years studied, with a mean of 2.60 litters produced per female. Production in Alberta varied from 2.47 litters per female in a year of decline to 3.52 litters per female in years of increase. These changes in Alberta were the combined effect of production of four litters by a large segment of the population in years of increase and variation in pregnancy rates. In New Brunswick the maximum number of litters per female was never more than three, and variation in pregnancy rates was less. In Alberta, one case of reproductive activity by a female young-of-the-year was recorded (Keith and Meslow 1967). This was not observed in New Brunswick, where evidence indicated that yearling hares were somewhat less active in reproduction than older adults. This was not demonstrated elsewhere.

Survival of various cohorts in the New Brunswick population showed the same degree of variation as in Alberta, but survival rates in New Brunswick were always somewhat higher than with Alberta hare populations. Adult and juvenile cohorts displayed major changes in survival rates in both areas.

Population fluctuations in New Brunswick hares resulted from variation in adult and juvenile survival, with changes in reproductive output playing a less significant role.

Keith (1974) recently suggested that the ultimate controlling factor on hare population cycles could prove to be the quality and quantity of food available, and that demonstrated changes in production and survival were basically a result of major changes in food supplies. Windberg and Keith (1976) have presented sound evidence to substantiate this theory.

The present study did not delve deeply into relations between hares and their food supply in New Brunswick. Subjective observation suggests, however, that the biomass of New Brunswick forests is much less able to support high densities of snowshoe hares than the forests of central Alberta. This might explain the lower general abundance of hares in New Brunswick, as well as the less pronounced population fluctuations.

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