Ecology of the Snowshoe Hare (*Lepus Americanus*) in the forests of the Maritime Provinces of Canada

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ECOLOGY OF THE SNOWSHOE HARE (LEPUS AMERICANUS) IN THE FORESTS OF THE MARITIME PROVINCES OF CANADA.

by

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OBJECTIVES

1. To define and study the circumstances under which snowshoe hare feeding can result in damage to commercial forests, and to determine the effects of various forest management programs on populations of snowshoe hares in the Maritime Provinces of Canada.

2. To study the population dynamics of the snowshoe hare in the Maritime Provinces, specifically reproduction, natality and mortality; determine seasonal and annual changes in these factors; and study the effects of these changes on fluctuations in hare density.

3. To determine hare utilization of the different forest habitat types, and study the food habits of the hare in the Maritime Provinces; to attempt to relate changes in habitat utilization and food habits to changes in habitat, season and population density.

4. To study dispersal, home range and movements within a hare population in the Maritime Provinces, and assess differences in these factors at different population densities.

JUSTIFICATION

Herbivorous mammals form an integral part of the natural forest communities of eastern Canada, and undoubtedly acted as a selective agent in their evolution. Human influences have modified those communities and will do so at an increasing rate in the future, profoundly affecting forest mammals. Increased investment in forest management leading to forests with more simplified composition of species suggests the possibility of increasingly serious damage problems. The basic objective of the forest mammal study group in Fredericton is to determine the interrelationships of forests and the mammals which inhabit them. The need to determine the part of the snowshoe hare in these interrelationships is the primary justification for this study.

The snowshoe hare has been studied little in the wild in the Maritime Provinces of Canada, and many questions remain unanswered. This study has been designed to contribute to the knowledge of habitat preferences, population dynamics, food habits and other factors in the ecology of the snowshoe hare in the Maritimes.

REVIEW OF LITERATURE AND RELATED WORK

I. INTRODUCTION

Lepus americanus Erxleben is primarily an animal of the boreal forests. It is a nocturnal, secretive creature, well adapted to forest life. It is commonly known as the snowshoe hare or varying hare in different parts of Canada, because of its marked seasonal color change and its well-furred hind feet which allow it to travel easily on the softest snow.

Snowshoe hare populations show violent fluctuations in numbers well-known as the basis of the ten year game cycle in northern boreal forests. Fluctuations between cyclic lows of 1 hare per square mile and highs of 30,000 hares per square mile have been described (Keith, 1963). Despite the magnitude of this cyclic phenomenon, the wide range and the relative ease with which it may be studied, little concentrated research has been done on the snowshoe hare, particularly in the Maritime Provinces. This review includes most of the significant work on the snowshoe hare, and also refers to other Lagomorpha where applicable.

II. TAXONOMIC STATUS OF THE SNOWSHOE HARE (Hall & Kelson, 1959)

Order Lagormorpha -- hares, rabbits and pikas
    Family Ochotonidae -- the pikas
    Family Leporidae* -- rabbits and hares
        Genus Oryctolagus** -- European rabbit

Genus Romerolagus --- Valcano rabbit of Mexico

Genus Sylvilagus --- Cottontail rabbit

Genus Lepus --- hares

1) Lepus arcticus --- arctic hare

2) Lepus othus --- Alaskan hare

3) Lepus townsendii --- white-tailed jackrabbit

4) Lepus californicus --- black-tailed jackrabbit

5) Lepus alleni --- antelope jackrabbit

6) Lepus insularis --- Black jackrabbit, Espiritu Santo Isl., California

7) Lepus flavigularis --- Tehuantepec jackrabbit - Mexico

8) Lepus mexicanus --- White-sided jackrabbit - Mexico

9) Lepus gaillardi --- Gaillard's jackrabbit - Mexico

10) Lepus europaeus** --- European hare

11) Lepus americanus --- snowshoe hare

* Four of the nine genera of Leporidae are found in North Ameri

** Introduced species.

The genus Lepus is divided from the eight Leporidae rabbit genera on the basis of skull characteristics, and the birth of Lepus young in an advanced state of development, with well-furred bodies and open eyes. Rabbit young are born naked, helpless and blind. Lepus americanus is the smallest of the hare species, and the only one adapted exclusively to life in wooded regions.

III. GEOGRAPHIC RANGE OF LEPUS AMERICANUS (Hall & Kelson, 1959)

The snowshoe hare has a wide distribution in northern North America (Fig. 1) extending across virtually all of Canada, excluding the tundra and arctic islands. Its range also extends into much of the northeastern United States, the Appalachian region, and the western mountain regions into California and New Mexico.

IV. AGE DETERMINATION

A number of methods have been used in hare and rabbit studies to separate juveniles or subadults from mature adults. Recent progress has been made into a technique for dividing adults into year classes.

1. Body Weight and Dimensions

Adults and subadults can be separated on the basis of body weight and dimensions. If one assumes constancy of growth and development in all young, such a technique has merits. However, differences in habitat, diet, condition of the mother and other variables may effect individual development, and cause wide variation in body dimensions.

Trapp (1962) found juvenile growth curves of Alaskan snowshoe hares leveled off at 1,000 g body weight and 139 mm hind foot length. Trapp found that hind foot length increased up to 80 days of age, while captive raised hares in Maine (Severaid, 1942) increased up to 110 days (136-138 mm). Trapp concluded that the best available method of age determination was a combination of body weight and hind foot length using only hares weighing less than 1,000 g (70 days) and hind foot length less than 100 mm (40 days).

Tiemeier (1965) found body weight could be used as an age criterion for juvenile black-tailed jackrabbits in Kansas until five months of age. Lord (1963) found body weight a reliable estimation of age in Illinois cottontails (Sylvilagus floridanus) until 100 days of age. Keith (unpublished) used weight and hind foot length measurements of captive and wildreared snowshoe hare juveniles to accurately age live trapped juveniles less than 90 days old.

Nelson (1909) observed in northern and mountain forms of snowshoe hares that the hind feet of adults were white while those of juveniles before the fall moult were brown. Adams (1959) found all adult Montana hares had some white on their hind feet in summer, while 93 percent of juveniles had none.

2. Epiphyseal Closure

Hale (1949) described a technique for aging cottontail rabbits by examination of the ossification stage of the epiphyseal cartilage of the humerus. Using a series of known age rabbits Hale determined that closure occurred at 7½ months. He suggested that the technique would be used with accuracy until January 1.

Lord (1963) found the average age of closure of Illinois cottontails was 7½-8 months, with a range of 5-15 months of age. Petrides (1951) and Wight (1957) found the average age of closure to be 7 months. Martinson et al. (1961) found the minimum age of closure in Missouri swamp rabbits was ten months, and they used closure to age large samples taken in January and February. Martinson et al. (1961) found no significant difference in the rate of closure in groups of pen raised and wild raised swamp rabbits (Sylvilagus aquaticus).

On the basis of epiphyseal closure, Lechlietner (1959) separated California black-tailed jackrabbits into three age classes: class I = 2-9 months, class II = 10-12 months, class III = greater than 12 months. Although data on black-tailed jackrabbits in Kansas (Tiemeier, 1965) indicated the change from class I to II occurred at 5 months, and from II to III at 14 months, Tiemeier found that he could distinguish the three classes of closure. Bronson and Tiemeier (1958) concluded that juvenile jackrabbits in Kansas could be accurately distinguished on the basis of epiphyseal closure until November. Closure occurred in this lagomorph at approximately eight months of age.

Using a combination of epiphyseal closure and condition of reproductive organs Flux (1967) found that all juvenile European hares in New Zealand could be distinguished until six months of age, many until eight months, and a few until ten months. Dodds (1965) determined epiphyseal closure dates for snowshoe hares as 225-235 days.

3. Condition of the genitalia

The external genitalia of snowshoe hares can be used to separate juveniles from adults during the first few months of juvenile life. Since virtually all adult females breed (Keith, 1965a), teat condition can be used to distinguish juveniles until they enter their first breeding season the spring after birth. Adams (1959) reported a high degree of accuracy using presence or absence of palpable teats in Montana hares. Keith reported that no females breed in their first summer of life, and that no juvenile females were found with palpable teats. Flux (1967) also reported using palpation of teats on European hares in New Zealand.

Male snowshoe hares have distinct penis characteristics by which juveniles and adults may be separated. Keith found in Alberta hares that the juvenile penis persisted until at least mid-January, and probably until the beginning of the first breeding season. Flux (1967) found similar penis characteristics in European hares of New Zealand.

4. Lens Weight

Lord (1959) described a technique for aging cottontail rabbits in Illinois based on eye lens growth. Lord assumed that the lens grows throughout life, and that individual variation in growth is sufficiently limited to allow accurate age determination. Eyes were removed immediately after death and fixed in ten percent formalin for a period of one week, which "was found to be sufficient" (Lord, 1959). The lens was then removed from the eye, dried at 80°C for 24-36 hours, and weighed. Lord considered the lens to be hygroscopic, and warned that weighing should be done immediately after removal from the oven. Friend (1965) later demonstrated that it was the glass vial in which the lens was dried and not the lens that was hygroscopic, and recommended that the vial and lens be allowed to cool ten minutes before weighing.

Lord found individual variation of dried lens weights to be only 0.87±1.21% (S.E.) within similar age groups. The curve of dried lens weights flattened at 73 days. Lord concluded that this technique could be used to determine month of birth of juveniles, and year of birth of adults.

Edwards (1962) collected 2,875 cottontail rabbits in Ohio on November 15, 1959, and aged them by the lens technique. He found a bimodal tendency in the lens data with the dividing point of adult and juvenile rabbits at 210 mg.

Friend (1965) made a thorough study of factors and variables affecting the lens aging technique. Using laboratory rats Friend described great differences caused by changing such variables as concentration of fixative, fixation time, and combinations of freezing and decomposition. Friend stressed the importance of technique standardization and understanding the variables involved in this technique.

Lord (1959 and 1962), Edwards (1962) and Friend and Linhard (1964) suggested that nutrition may play an important part in rate of growth of a lens. In a series of carefully controlled experiments using rats, Friend (1966) found no significant differences between lens weights and varying nutritional level diets. Friend also found no statistical correlation between lens weights and body weights in rats of similar sex and age.

Dudzinski and Mykytowycz (1961), using 71 known age rabbits found lens weights to be a reliable indicator of wild rabbit (Oryctolagus cuniculus) age in Australia until about 150 days of age. Martinson et al. (1961) found a range of juvenile lens weights of 128-205 mg and an adult range of 213-304 mg in Missouri swamp rabbits collected in December and January. They concluded that lens weight at this time of year was a valid criterion of swamp rabbit age.

Tiemeier (1965) concluded that lens weight was a superior technique in black-tailed jackrabbit age determination than techniques based on body size, body weight or epiphyseal closure because lens weight growth curves permitted determination of birth month in young. Dudzinski and Mykytowycz (1961) found lens weight a more reliable method of separating adult and juvenile European rabbits than body weight. Similar conclusions were made by Walhovd (1966) in Denmark and Flux (1967) in New Zealand for European hares.

V. CENSUS TECHNIQUES

A major problem in studying the ecology of a natural population is an accurate estimate of the population density. As with most wildlife species, a total count of snowshoe hare numbers is virtually impossible. The most widely used estimates of density for rabbits and hares are techniques based on live trapping data. Some use is also made of population indices such as track counts and fecal pellet counts.

1. Live trapping Methods

Live trapping is a relatively simple, albeit time consuming, task which requires much effort for a small amount of data. However, an accurate estimate of population numbers is prerequisite for many conclusions on population dynamics. Data on other aspects of life history such as sex and age ratios, reproduction, home range size and movements, and cover-type preferences are also gained from live trapping.

Population estimation by live trapping is based on the rate of recovery of marked animals by one of several mathematical formulae. The validity of this technique depends upon the following assumptions (Ricker, 1958) that:

1) Marked individuals retain their marks,

2) Natural mortality is the same within both marked and unmarked segments of the population,

3) Marked and unmarked animals are equally vulnerable to recapture,

4) Either the marking or the recapture is random,

5) Ingress, egress and/or recruitment are negligible between marking and recapture.

Several live trap types are used by hare and rabbit investigators, all of which probably do an efficient job, the choice depending on the individual worker. One popular type, made by the National Live Trap Co. of Tomahawk, Wisconsin, is a durable and light wire mesh construction which can be collapsed for ease of moving and storage.

Trap stations are generally located systematically with the aid of a grid, although some investigators prefer to locate trap stations in a random manner (Keith 1965a). In either case, once the station is selected, a certain amount of subjectivity is involved in choosing a particular site to set the trap. This is done by examining animal "sign" and choosing a spot where an animal is likely to be caught. For snowshoe hares, trap stations have been laid out on grids varying from 330 feet to 500 feet between stations (Adams, 1959; O'Farrell 1960 and 1965; and Bookhout, 1965a) with traps set within a certain distance of the station.

Trap baiting may introduce a bias into results by attracting and catching certain marked animals more often than unmarked animals. Many investigators disregard this effect and assume that capture rate is equal in both marked and unmarked segments of the population. Keith (1965a and 1966) felt he had eliminated this bias, by setting unbaited traps on hare runways and by constant trap relocation. His data show an apparent homogeneity of trap response. A variety of baits are described in the literature, but alfalfa hay has been emphasized as the best "standard bait" (Aldous, 1937; Green & Evans, 1940a; Adams, 1959; O'Farrell, 1960; and French et al., 1965) for hares.

Green and Evans (1940a) reported that live trapping in Minnesota was not possible in summer months. They suggested this was the result of a lack of bait attraction amind lush summer vegetation, and the absence of easily discovered runways in the forest of this area. Bookhout (pers. comm.) encountered the same situation in Michigan. Conversely, runways are quite distinct in all seasons in Alberta (Keith, pers. comm), Alaska (O'Farrell, 1960 and 1965), and New Brunswick (Wood, unpublished).

Keith (1965b) developed a snare for live capture of snowshoe hares in Alberta. During 1961-64, Keith snared 374 hares, of which 51 percent survived. He concluded that the live-snare was a convenient sampling method, with minimum effort and expense, and without 90-100% losses characteristic of regular snaring.

2. Marking

The most commonly used snowshoe hare marking method is an ear tag. Bider (1961) reported the only known loss of tags on Quebec hares (two plastic washers held together by a brass pin) occurred in traps, while Green and Evans (1940a) reported no irritation or loss with monel metal tags on Minnesota hares. O'Farrell (1960 and 1965) reported minimal loss of monel metal tags in Alaska.

Keith (1965a) used several marking methods in Alberta. All adults were ear tatooed, and small monel metal tags placed between the toes of each hind foot. Juvenile hares taken in the summer were systematically toe clipped, and at certain periods in winter all hares were rump dyed with picric acid or rhodamine B solutions. During early spring all pregnant females were implanted with radioactive Ca^{45} capsule (Rongstad, 1965). Tatoos, when properly applied lasted for the life of the hare. The toe tags served for identification when predator remains were found on the study area. Rump dying served in visual recognition of hares flushed during the winter. The gelatinous Ca^{45} capsule implanted subcutaneously broke down and resulted in recognizable levels of radioactivity in all young born of those females during that breeding season. The toe clipping of all juveniles in the summer provided material which was ashed for radioactive counts.

3. Trap-retrap Estimates of Population Density

Green and Evans (1940a) live trapped more than 5,000 hares in Minnesota from 1932 through 1939. The period from early autumn to early spring was the "precensus trapping period," and a 2½ week period in April was the "census period". Using the principle of the Petersen-Lincoln Index (Ricker, 1958) green and Evans estimated the average mid-winter hare population levels of their study area. They felt the sedentary nature of the snowshoe hare made emmigration of marked animals negligible, and that their estimates were reliable.

Bookhout (1965a) trapped snowshoe hares in Michigan for 16 months beginning in December, 1959, and estimated hare density monthly by both the Petersen-Lincoln Index method and the Frequency of Capture methods (Schnabel Multiple Census Method and Schumacher-Eschmeyer Multiple Census Method - Ricker, 1958). The Petersen-Lincoln Index and the Frequency of Capture methods gave similar estimates for most months. Bookhout's trapping effort was sufficiently extensive to give a relatively high proportion of recaptured animals, allowing satisfactory confidence to be placed in the results.

Keith (1966) used the Petersen-Lincoln Index for density estimates of Alberta hares, always using at least two independent estimates for each census period. Keith felt the Petersen-Lincoln Index to be most applicable to snowshoe hare populations.

O'Farrell (1960 and 1965) and Trapp (1962) compared census methods for Alaskan snowshoe hares. Both found that estimates from the Petersen-Lincoln Index and the Schnabel method were similar, but confidence limits were too wide to achieve statistical accuracy. Their study area was only 160 acres in size, and thus the study population of the area was probably too small. Their trap effort was low, giving too few recaptures, which may account for the inaccurate results.

Edwards and Eberhardt (1967) took extensive trap-retrap data from two known cottontail populations of 130 and 135 rabbits each, and applied several estimating equations. The results showed that the Schnabel and Schumacher-Eschmeyer methods grossly underestimated the populations: Both were considered unsatisfactory for estimating rabbit numbers from live trap data. Estimates obtained from a Maximum Likelyhood Estimation (MLE) based on the Poisson distribution also underestimated the populations. The MLE equation based on a geometric distribution overestimated the population somewhat. The best population estimate was derived from an equation of linear regression based on a geometric distribution. Edwards and Eberhardt recommended the linear regression and MLE of the geometric model equations with a capture rate of 50 percent of population and an average capture per animal of 1.5-2.

4. Other Census Techniques Based on Live Trapping

Adams (1959) described a Calendar Graph for estimating hare population density. By plotting the known history of each marked hare on his island study area, Adams was able to calculate the number of marked hares on the island at any time during the study. This estimate may not be as suitable on large expanses of unbroken habitat, because immigration and emmigration would be important factors. The Calendar Graph did give Adams a minimal population figure for his island.

O'Farrell (1960 and 1965) and Trapp (1962) found the Calendar Graph was only an estimate of the minimum size, with no value in indicating the true size of the hare population. These results may have been influenced by the small study area, small sample size and low trap effort mentioned earlier.

Methods based on rump dyed rabbits and hares have been used by Lord (1963) on cottontail rabbits, and Keith (1965a) on Alberta snowshoe hares. Both used picric acid and rhodamine-B, which have good retention qualities, to mark live trapped animals before release. Keith made use of English rabbit nets twice each winter to capture large numbers of hares. Both used a drive-census to determine proportions of marked to unmarked individuals. Population estimates were made by the Petersen-Lincoln Index. This method eliminates the bias of differential trap response from the estimate.

The Ca^{45} implantation method (Rongstad, 1965) has been used extensively by Keith (1965a) who feels it provides the most independent estimate of spring hare populations. The short half-life of Ca^{45} (163 days) ensures no carry-over to the next breeding season, and the method provides an increased number of marked animals per trap effort while eliminating retrap bias.

5. Population Indices

(a) Trap Success

Keith et al. (1966) found that 1961 was a peak year for hares in Alberta, and the next three years were years of population decline reaching a low in the spring of 1964. The estimated population densities in April and December 1962, and April and December 1963 were 629, 297, 212, and 73 hares per square mile respectively. The population was so low in 1964 that no statistical estimate was possible. Trap success data expressed as captures per 100 trap nights in April and December 1962, April and December 1963, and April 1964 were 36.0, 11.7, 17.7, 3.7 and 1.6. Keith found that trap night indices corresponded closely to other population estimates.

(b) Fecal Pellet Counts

MacLulich (1937) estimated hare population levels throughout wide areas of Ontario by counting fecal pellets. He assumed that hares defecate while feeding or shortly after, and that pellets would be found in association with important feeding areas. He felt that one year's droppings would disintegrate and become buried before the next summer, but that the few which did persist until the next summer could be easily recognized. MacLulich thus counted all "recent" pellets on 25-0.2 square meters plots in each census area and used these data in density calculations.

Adams (1959) felt that pellet counts were less costly than other census methods, and allowed analysis of a population by habitat or other subdivision of the range. Adams felt that hare fecal pellets were distributed at random, and pellet counts were valid estimations of hare density. He established 316-1/10,000 acre plots, cleared the old pellets in June 1953, and made counts in July, August, September and November 1953, and January, March, April, May and July 1954. These pellet counts related closely to recapture population estimates although biases due to age of the hare and food eaten may have been present.

Hartman (1960) did some extensive work with pellet counts in Ontario. She estimated deposition rate, loss of pellets in litter, and weathering losses in different litter types from data on caged and field enclosured hares. Hartman cleared a number of quarter millacre plots in November, 1958, and made new pellet counts in May, 1959. The population estimate derived from pellet counts was very close to the estimate derived from recapture methods.

O'Farrell (1960 and 1965) and Trapp (1962) made pellet counts in the fall on 20-1/10,000 acre plots in Alaska. Results were inconclusive because too few pellets were collected, reflecting the paucity of sample plots used.

Taylor and Williams (1956) estimated wild rabbit (Oryctolagus cuniculus) numbers in New Zealand from the density of fecal pellets on the ground, making allowances for pellet production rate per rabbit, and decay rate of pellets. Lord (1963) used cottontail pellet density to analyze habitat utilization of three crop types in Illinois, sampling 300 quadrats 2' x 1' in each crop type. Lord found pellet deposition rate varied according to a number of factors including food type, season, sex and age, and was not a good criterion of estimating population density. Disappearance rate in the various habitats also varied from 4.00% per day to 7.69% per day. The major factor in disappearance was not rain, but incidence of earthworms.

(c) Track Counts

Hartman (1960) studied snowshoe hare density in Ontario by counting tracks after a snowfall. Using 27.6 miles of line transects, counts were made the day after a snowfall. Numbers of hares using each track crossing the transect were rated as one, two, or three plus. The number of tracks per chain were closely correlated to estimated population levels. Hartman concluded that track counts, taken repeatedly on a single area, indicate relative abundance of hares.

In Alaska, O'Farrell (1960 and 1965) found almost no hare trails the day after a fresh snow, and two days after a fresh snow trails and runways were too well used to permit an accurate count of individual trails. O'Farrell concluded that in low population densities a track count index might be useful, but as the population increases this method becomes less useful for census purposes.

Hartman (1960) suggested that a toe clipped pattern on snowshoe hares would be distinguishable after a fresh snow. Trapp (1962) toe clipped 38 hares in Alaska and found that clipped and unclipped tracks could not be distinguished in dry snow.

(d) Strip Census

Webb (1942) proposed a method for censusing snowshoe hares based on King's (in Webb, 1942) census technique for grouse. Transect lines were walked, and the "jumping angles" and flushing distances calculated for all hares seen. Webb then estimated hares per square mile from these data. This method was used with great success for black-tailed jackrabbits in Kansas by Tiemeier (1965), who felt that the conspicuousness of jackrabbits on the short grass prairie made this method of direct counting quite reliable. MacLulich (1937) used this method in Ontario for censusing snowshoe hares, and expressed his results in density per square mile. In Alaska, O'Farrell (1960 and 1965) and Trapp (1962) attempted to census snowshoe hares by this method, but found that the hare's habit of "freezing" rather than flushing (also noted by Seton, 1953 and Adams, 1959), and their protective coloration made the transect count unreliable.

(e) Roadside Counts

Much investigation has been carried out on estimating numbers of cottontail rabbits by making evening or morning counts on roadsides. Lord (1963) reported the results of extensive roadside estimating on cottontails in Illinois. Accounting for seasonal changes in activity, weather, light conditions and topographical features, Lord found that annual roadside activity was directly correlated with sexual activity, and inversely correlated with the height of the herbaceous vegetation. Lord felt his estimate was reliable because he drove the same 20-30 mile routes at the same times every year.

Trapp (1962) found that road counts were affected by many variables in Alaska, such as weather, sexual activity, traffic, and attractiveness of salts and minerals on the road. Trapp felt that the procedure was impractical for snowshoe hares, with gross results of questionable validity.

VI. HOME RANGE, MOVEMENTS AND BEHAVIOR

1. Home Range and Movements

Most authors who have worked on the snowshoe hare agree that it is sendentary in nature, with a remarkably restricted home range, despite considerable potential for dispersal. Table 1 shows home ranges of the snowshoe hare on different parts of its range. It should be noted that the methods used by the different authors for estimating ranges were not constant, and statistical comparisons of the results are not valid.

The data in Table 1 represent periods during different seasons, and of differing lengths, and thus some variation will be seen. Keith (1965a) observed, that depending on the season and the time span considered, home ranges of snowshoe hare varied between 5 and 40 acres.

All things considered, data in Table 1 indicate that the snowshoe hare has a small home range.

Criddle (1938) reported the radius of movement of the snowshoe hare as "a few hundred yards in dense woods to a mile or more in thin woods". MacLulich (1937) reported a radius of movement of only a few hundred yards, and Aldous (1937) observed that 69 percent of his recaptures were within one-eighth mile (220 yards) of the original capture point. Adams (1959) reported an average distance between captures of 118 yards for adult males, 76 yards for adult females, 67 yards for juvenile males, and 66 yards for juvenile females. O'Farrell (1960 and 1965) observed that 89 percent of his recaptures in Alaska were within 1,000 feet of the original capture point. Trapp (1962) calculated a mean adjusted range length of 383 yards for 26 hares in O'Farrell's study, and 358 yards for 31 hares in his own study in Alaska.

Bookhout (1965a) reported average daily movements in winter of 156 yards for adult males, and 121 yards for adult female snowshoe hares in Michigan. The daily movements of only 6 of 272 females and 14 of 602 males observed by Bookhout exceeded one-quarter mile (440 yards). The longest daily movement recorded by Bookhout in winter was 739 yards for males and 931 yards for females. Bookhout found daily movements to be greater in summer, the average for males being 194 yards and for females 191 yards. The longest daily movements in summer were 673 yards for males and 594 yards for females. Keith (1965a) recaptured 265 hares one year after marking in Alberta, and found that 50 percent had moved less than 110 yards, 75 percent less than 220 yards, and 97 percent less than 440 yards from the original point of capture. The longest recorded movement of a snowshoe hare in the literature was a female marked as a juvenile in August 1958 by O'Farrell (1960), and shot by a hunter in September 1959, 12.5 miles away.

These movement data substantiate the conclusion drawn from home range estimations that the snowshoe hare leads a sedentary life, with long movements being rare.

2. Territoriality

Grange (1932) and MacLulich (1937) found little evidence of territoriality in snowshoe hares in the wild. Criddle (1938) trapped no hares with torn ears or bites around the head, and concluded that aggression among hares must be very rare. This indicates a lack of territorial behavior within the species. Severaid (1945), working with captive hares, observed that 90 percent of individual hares could be expected to tolerate one another even under close confinement.

All reports in the literature have agreed that the home ranges of snowshoe hares overlap greatly. Bookhout (1965a) observed this great overlapping of ranges and suggested that size of home range might be density dependent as Toll et al. (1960) found in swamp rabbits. Bookhout reported hares to be very tolerant of each other even in the breeding season and concluded that territories, if they exist, are quite small.

Adams (1959) recorded that hares did show a certain resistance to crowding and were well dispersed, with no tendency to herd or flock. He concluded that hares may have a territory falling into Dice's (1952, p. 247) number seven; the area around the animal itself.

3. Use of Burrows, Nests and Forms

Audubon and Bachman (1851) reported that snowshoe hares do not take shelter in holes in the ground or in hollow trees, and Richardson (1829) observed that hares do not burrow. Grange (1932), MacLulich (1937), and Criddle (1938) stated that hares make use of existing hollow logs and holes in the ground, but do not themselves burrow. Criddle concluded that the chief value of burrows to hares was in escape from birds of prey, as they seldom used them when pursued by dogs or wolves.

Audubon and Bachman (1851), Cory (1912) and Klugh (1926) believed that young hares are born in nests of grass lined with fur from the mother's body, and Bachman (1851) recorded a captive litter born in such a nest. However, Seton (1953) believed that hares build no nest, and Grange (1932) and Aldous (1937) found no evidence of nest construction. Adams (1959) excavated several burrows used by hares which he thought had been made by badgers, and found no nest, rest chamber or any other modification attributable to hare use.

Aldous (1937) and Trapp (1962) observed that hares used forms, or simple oval depressions in ground litter under good cover, as resting places. Both authors reported that these forms were used year round. Trapp observed that in winter forms were found under snow laden branches bent to the ground and in bowl-shaped depressions at the base of spruce trees.

4. Effects of Weather, Season, Age, Sex and Habitat

Lord (1963) stated that the size of home range, and presumably the extent of movement of a terrestrial mammal like the cottontail rabbit depends upon the habitat, season, sex and age of the animal. Dalke and Sime (1938) in Connecticut, and Schwartz (1941) in Missouri observed that adult female cottontails have smaller ranges than adult males. Haugen (1942) reported that female cottontails in Michigan have larger ranges in the breeding season than the non-breeding season.

Male snowshoe hare ranges in Michigan (Bookhout, 1965a) averaged 38 percent larger in summer than in winter, while female ranges remained almost identical. O'Farrell (1960 and 1965) found that home ranges of hares in Alaska did not change significantly in size in the early breeding season, but the animals apparently became more active, resulting in an increased use of the range, as indicated by an increase in capture rate.

Bookhout found in his work with snowshoe hares in Michigan that summer ranges were merely extensions of winter ranges. Where shifts in range did occur, in most cases they represented a shift within the same cover type and not a movement to a new cover type. French et al. (1965), working with black-tailed jackrabbits in Idaho, found that despite a great dispersal potential, extensive seasonal shifts of home range did not occur.

Bookhout also observed that male snowshoe hares had significantly larger home ranges than females, which is similar to Adams' (1959) data (Table 1). Bookhout found that five of 38 adult males had ranges larger than 40 acres, while no female range exceeded 35 acres. Adams' data also show that juvenile animals have much smaller ranges than do adults.

Trapp (1962) found that Alaskan snowshoe hare movements were restricted by weather, with trap success falling by about 50 percent following rain or snow. O'Farrell (1960 and 1965) in Alaska and Bookhout (1965a) in Michigan made similar conclusions concerning snowfall, and Trapp also noted reduced activity during severe cold weather (below -30°F). Tiemeier (1965) concluded wind was the most important factor influencing activity of black-tailed jackrabbits in Kansas, and reported that rain and temperature seemed to have little effect on movement.

Bider (1961) concluded that wind and light intensity were the main restrictive factors on winter movements of snowshoe hares in Quebec, but in summer these factors did not seem to play a critical role on regulation of movements. Bider's results on the effect of rain are inconclusive, and he found that snow did not impede hare mobility.

Criddle (1938) noted that snowshoe hares in Manitoba make extensive use of runways during winter, frequently packing them by hopping up and down to give a good solid surface. Grange (1932) also described heavily used runways in Wisconsin. Bider most frequently found runways in conifers. He believed they were used as a convenience between browsing and cover areas, and indicated poor browsing habits on the part of the hare. In Alaska, O'Farrell observed well used runways in summer as well as winter, and described their differing characteristics with changing snow conditions. In early winter when the snow was light, well packed runways were common, and single trails rare. As the snow compacted, single trails were seen everywhere, and well packed runways were rare. During the April thaw the density of the snow changed still further and hares used runways almost exclusively. These findings are in agreement with those of Pruitt (1960) who observed hares using well packed runways when snow density fell below a critical level.

In Michigan, Bookhout (1965a) never observed a well used runway. He occasionally found trails with three or four sets of tracks, but never the type of well packed runway described by other authors. Bookhout agreed with Grange (1932) that runways are probably used as a means of convenience in travel, but he found no evidence to support Bider's (1961) theory that runways indicated poor browsing habits. Bookhout believed that well used runways indicate high hare density. Densities in his Michigan study never exceeded one hare per 3.9 acres, and Bookhout supposed that much greater densities than this were necessary to show heavy runway use.

VII. HABITAT UTILIZATION

Early naturalists observed that snowshoe hares were found "mostly in willow thickets" in northern districts (Richardson, 1829) and in swamps in Ontario (Miller, 1897). Seton (1909 and 1953) reported that the preferred habitats in Manitoba were tamarack and cedar swamps, and willow thickets. Questionaire replies from local residents analyzed by MacLulich (1937) indicated that in Ontario the "typical habitat" for snowshoe hares was cedar, spruce and alder-willow swamp. Jack pine forests, where they predominated, were also important hare habitat. The questionaires indicated that in Quebec and the Maritimes no one habitat type was used more than others. In western Canada, where coniferous swamps rarely occur, willow-alder swamps and thickets were reported as the chief hare habitat. Upland spruce forests and jack pine were also important for hares in western Canada.

MacLulich's Ontario population density calculations indicated that at the population peak in July 1932 the density in other areas was as great as in the conifer swamps (about 3,300 per square mile). By September 1932, the density of other habitats had declined to 200 per square mile, but only to 950 per square mile in the swamps. 1933 and 1934 were years of population decline in Ontario, with the low point in the cycle in the summer of 1935. During these three years the swamp habitat had hare densities of 70, 80 and 30 per square mile, while the other habitat had densities of 25, 0, and 0. Keith (1966) documented a similar vacating of habitat during the 1962-1964 population decline in Alberta. Keith noted progressive shrinkage of hare range, with the first sections devoid of hares having the least amount of brushy cover. The two areas still occupied at the population low in 1964 were a burned over tangle of deadfalls and raspberry with dense regrowth of young aspens and willows, and a bog edge thicket area of small black spruce, alder and patches of hazel.

Grange (1932) observed that snowshoe hares in Wisconsin were less frequent in mature woodlands of any type than in young, bushy growths with good food and cover. Grange noted that the most extensively used habitat types were aspen areas, alder swamps and conifer swamps. Other vegetative types used extensively were young cedar stands, young jack pine stands, and old burns, particularly where there was a profusion of raspberry, logs, aspen shoots and other low vegetation. Hare rarely used mature hardwoods in any season of the year unless beaver were present, and then they made use of waste left by the beaver.

Bider (1961) found greatest snowshoe hare movement in white cedar, black spruce bogs and upland spruce-fir areas of Quebec. Bookhout (1965a) observed that swamp conifer was by far preferred in Michigan, and conifer areas generally outweighed other major habitat types. Bookhout listed the following habitats by hare preference: pure stands of swamp conifer and alder swamp, high preference; aspen-balsam fir-paper birch, of moderate preference; mixed swamp hardwoods and conifers, relatively low preference; northern hardwoods, very low in hare use; grassy openings, little or no use. Bookhout noted that hare preference seemed to depend mostly upon the amount of brushy undergrowth for food and cover.

VIII. PHYSIOGRAPHIC INFLUENCES

Several authors have suggested a correlation between physiological vigor, reproductive performance, and fertility of the soil in the area where cottontail rabbits live. Rowe (1947) in Missouri, and Bruna (1952) in Kentucky demonstrated a greater body weight in cottontail from fertile than from poor soils. Williams (1964) disputed these findings: after considering the factors of season, time of day collected, and age and sex of a Missouri cottontail sample, he found no positive correlation between body weight and soil fertility. Williams concluded that because of certain limitations in the data of Rowe and Bruna, the question of a positive correlation between cottontail body weight and soil fertility was not demonstrated convincingly.

Edwards (1962) tested the correlation between cottontail reproductive performance and soil fertility in Ohio. A total of 2,876 rabbits were aged by the eye lens technique and the sample from a fertile limestone-soils region had a significantly higher proportion of juveniles than the sample from a poor unglaciated-soils regions, indicating that cottontail reproduction and/or survival was better in the limestone-soils region. This was in agreement with the findings of Negus (1956) and Stevens (1962) who found larger litter sizes from the limestone-soils region of Ohio. Edwards' data also indicated that cottontails from the limestone region had a more prolonged period of high reproduction, with a larger proportion of breeding juveniles and higher reproductive success in the juveniles. Williams and Caskey (1965) collected similar results for Missouri cottontail litter size and concluded that the lower soil fertility resulted in nutritional deficiencies which manifested themselves in the cottontail through reduced reproductive output.

IX. REPRODUCTION

1. Mating Behavior

In snowshoe hares, mating chases begin in February, apparently preceding successful mating by one month or more. Dodds (1965) noted that this premating behavior in captive hares indicated an increasing intensity in male aggressiveness, and that the beginning of this aggressive behavior was positively correlated with an increase in testes size. Dodds concluded that this behavior was not necessarily an indication that successful mating was occurring in the wild.

Bookhout (1965b) observed that snowshoe hares, like the European rabbit, commonly urinated on their partners during premating activities. Evidence of such activity was clearly visible in the snow, and Bookhout suggested that it may indicate the initiation of the breeding season.

2. The Breeding Season

(a) Onset and Duration of Breeding

Lyman (1943) observed that breeding chronology in mammals such as hares is governed exogenously by increasing day length and endogenously by a basic rhythm. Bookhout (1965a) observed that males are capable of breeding some six weeks before females, and thus the onset of breeding is triggered by the females. Keith et al. (1966) noted that the onset of breeding was closely synchronized in all females, with the initial conception peak occurring in the first two weeks of April. The time of onset is remarkably similar through the entire range of the hare (Table 2). Only in central Alaska, where the initial conception peak is about two weeks later, does this regularity in initial onset not hold. Keith et al. also noted that the termination of breeding occurs widely at the same time, late July and early August (Table 2).

Adams (1959) and Keith (1966) concluded that females lactate continuously throughout the breeding season. Severaid (1942) observed weaning of young at 25-28 days, but the last litter of the year may be nursed up to 56 days (Severaid, 1942 and Adams, 1959). Adams observed the first lactating female on April 28, and the last on September 22, and between the birth of the first and last litters, only three percent of adult females taken were non-lactating. This also indicated to Keith and Adams that at the height of the season, virtually all females were breeding.

(b) Synochrony of Conception and Parturition

Keith (1965a and 1966) and Keith et al. (1966) observed a very closely synchronized onset of breeding among female hares in Alberta. Immediate post-partum breeding appeared to be the rule, resulting in clearly defined litter groups. Mean conception dates for the litter groups (Keith, 1965a) were in the second week of April, mid-May, and the third week of June (1961-1964). In 1961 and 1964, fourth litter groups occurred in mid-July. Bookhout (1965a and 1965b) found a well defined initial conception peak from April 1-15 in Michigan, and a second peak of conception of smaller magnitude distributed over a period of approximately 45 days from May 16-31 to July 1-15. Bookhout concluded that the majority of females bred for the second time shortly after the birth of their first litters, and that the occurrence of third litters accounted for the extended conception period after May 15. Newson (1964) found three well synchronized peaks of conception in early April, mid-May and late June in Ontario, with sometimes a slight fourth peak in July. In Maine hares, Severaid (1945) also found post-partum breeding to be the rule.

Adams (1959) concluded that dates of first pregnancy in Montana hares ranged over 3-4 weeks. Dodds (1965) concluded that his data did not show a high degree of synchrony of conception dates in Newfoundland, although they were grouped essentially into three main periods, the end of April, late May--early June, and late June--early July. Dodds suggested that most hares did not begin breeding until sometime after the earliest conception date, that the onset of breeding was gradual and that continuous pregnancy occurred from mid-April until early August. These findings of Adams and Dodds are at variance with those of Keith, Bookhout and Newson.

Synchrony of conception dates and post-partum breeding have been commonly attributed to the cottontail rabbit (Lord, 1961b; Conaway and Wight, 1962; Conaway et al., 1963; Marsden and Conaway, 1963; and Evans et al., 1965), and the English rabbit (Thompson and Worden, 1956). Conaway and Wight postulated a fourteen-day cycle of recurring pre-estrus periods to explain the synchronous conception periods in Missouri cottontail rabbits. Evans et al., however, found that a fourteen-day cycle did not fit the pattern of conceptions of their Missouri cottontail populations, and suggested a seven-day cycle, or multiples thereof, of recurring pre-estrus. Marsden and Conaway found a seven-day behavioral cycle in cottontails, and a pre-estrus cycle of this length might be expected. Myers and Poole (1962) also observed that females were sexually active and mated at intervals or multiples of seven days in confined populations of Australian wild rabbit. This cycle appeared to continue into pregnancy and was not interrupted by resorptions.

3. Male Reproductive Cycle

Accounts from Newfoundland (Dodds, 1965), Ontario (Newson, 1964), Michigan (Bookhout, 1965b), Minnesota (Aldous, 1937), Alberta (Keith, 1965a), and Alaska (Trapp, 1962) indicate that the snowshoe hare breeding season is initiated and terminated at about the same times all across North America. Testes weights begin gradually to increase in January while the testes are still abdominal. In February the testes descend into the scrotum and increase rapidly in size. Spermatogenesis begins to appear in February and by March most males are in stages of active spermatogenesis. Maximum testes weights occur in May, then there is a gradual decrease in weight until July when a rapid decline occurs. The testes are abdominal and at minimum weight by September and they stay in this inactive state until the following January. Similar annual rhythms have been described for jackrabbits (Bronson and Tiemeier, 1958 and Tiemeier, 1965), European hares (Flux, 1967 and Raczynski, 1954) and cottontail rabbits (Ecke, 1955).

Most investigators felt that testes weight and position were not reliable indicators of sexual activity in male snowshoe hares (Aldous, 1937; Newson, 1964; Bookhout, 1965a and 1965b; Dodds, 1965; and Keith, 1965a), and used sperm smears or paraffin sectioning to rate spermatogenesis. Keith felt, however, that an average single testis weight below four grams indicated cessation of fertility in males. Keith was doubtful that reproductive capabilities of male hares could be assessed solely on the basis of sperm content of the cauda epididymides since the epididymides does store sperm well after production has ceased (Lechlietner, 1959). He felt that breeding is probably contingent upon the loss of libido or potency in males, and his data support his suggestion that hormonal changes at cessation of breeding are closely reflected by testis weight. Thus Keith feels that an average testis weight above four grams in July indicates reproductive activity, and below four grams indicates cessation of activity.

Bronson and Tiemeier (1958) and Tiemeier (1965) used sperm smears to rate the reproductive capacity of jackrabbits in Kansas and reported that sperm production was generally confined to males with a paired testes weight greater than five grams. Raczynski (1964) used sperm smears as the criterion of sexual activity in male European hares in Poland and he did not correlate activity with any particular testis weight. In the same species in New Zealand, Flux (1967) felt that a testis weight greater than five grams indicated sexual activity. Ecke (1955) found the best criterion of breeding condition in Illinois cottontails was the amount of sperm in the epididymides, and he did not correlate this with a testes weight because of a wide weight range during the breeding season.

Male snowshoe hares do not breed in the summer of their birth (Aldous, 1937 and Keith, 1965a), whereas male European hares do (Flux, 1967). Flux found that 15 percent of the juvenile European hares he examined in January and February in New Zealand were capable of breeding, with testis weights above five grams. However, the European hare has a breeding season lasting 10½ months in New Zealand, whereas the snowshoe hare breeding season is less than half this time.

Aldous observed that the penis of snowshoe hares was pale pink in the nonbreeding season and a bright red in the breeding season. Trapp (1962) noted a distinct morphological difference between the juvenile and adult penis, and stated that the penis did not attain adult form until approximately 200 days of age. He used these penis traits to age hares until the end of November. Keith (1965a) observed that these penis traits were definitely reliable for aging Alberta hares until January, and probably until the start of the breeding season.

4. Female Reproductive Cycle

The female cycle of the snowshoe hare has been studied less than the European rabbit, and since the reproductive physiology of the two is essentially the same, a brief description of the European rabbit is included here (Marshall, 1922; Hammond and Marshall, 1925; and Allen, Danforth and Doisy, 1939).

During the winter months the females are in an anoestrus period when follicular growth in the ovaries is greatly suppressed. The follicles develop to a certain point, but maturation does not occur. At the end of anoestrus, an external stimulus causes Follicle Stimulating Hormone (FSH) to be secreted by the pituitaries, which stimulates follicular growth in the ovaries. The ova develop to submature stage during which time the rabbit is said to be in heat.

The nervous stimulation of coitus causes the pituitaries to secrete Luteinizing Hormone (LH) which causes erruptive follicular growth. Ovulation occurs about ten hours after coitus. The ova are fertilized in the Fallopian tube and the fertilized ova enter the uterus on about the fourth day, becoming implanted on about the seventh day.

Soon after ovulation occurs, corpora lutea form at the sites of the follicular ruptures and remain through the duration of the pregnancy. As long as the corpora lutea are active, they secrete progesterone which inhibits the formation and ovulation of other mature ova. Towards the end of pregnancy the corpora lutea start to decrease in size, and the placentae take over the secretion of progesterone. Within a few hours after parturition and the subsequent stop of progesterone secretion, mature follicles again appear in the ovaries. It is thus common for rabbits to have fertile coitus very soon after parturition.

Newson (1964) noticed that during the winter months the parous uterus of the adult hare could be distinguished in size and appearance from the nulliparous uterus of sub-adults, and she used this characteristic to age females in the winter. Newson (1964) and Dodds (1965) found macroscopically visible follicles in snowshoe hare ovaries in early March, and from mid-March to August maturing follicles were present. Beginning in late August, follicles became atretic and failed to mature.

Audubon and Bachman (1851) reported the snowshoe hare gestation period to be about six weeks. Grange (1932) found it to be thirty-six days, or perhaps a few hours more. Observing gestation in 37 captive hares, Severaid (1945) found it ranged from 36 to 40 days, with a mean of 37.2. Dodds found that eight captive females were pregnant for 36.6 days (Range 34-38 days). Most recent investigators accept 37 days as the length of the snowshoe hare gestation period, with implantation of the ova occurring on about the seventh day after conception.

5. Size and Number of Litters

There is a well known tendency among rabbits and hares for first litters to be smaller than subsequent ones (Severaid, 1942; Thompson and Worden, 1956; and Conaway and Wight, 1962). Keith et al. (1966) presented all the available data on wild snowshoe hare reproduction (Table 3) and they indicate that first litters are indeed smaller than subsequent ones in snowshoe hares. Dodds (1965) found that although the average first litter sizes were smaller for all years and areas studied in Newfoundland, this relationship did not always hold true in different regions for particular years. Table 3 also shows a wide range in litter size and a tendency to increase with latitude.

Aldous (1937) observed a female hare in Minnesota which mated 11 days after parturition. Using a gestation period of 36 days (Grange, 1932 and assuming this female to be average, Aldous calculated that it would be possible for female hares to have four litters per season. Severaid (1945) observed the reproductive patterns of 16 captive female hares in 1941. Of these, 100 percent had first litters, 87.5 percent had second litters, 56.25 percent had third litters and 37.5 percent had fourth litters, for an average number of litters per female of 2.75. A similar figure for 1940 was 3.0 litters per female.

Green and Evans (1940c) devised a method for estimating the total production of young per female per year which considered seasonal change in proportion of pregnant animals in the population. Collecting effort was kept approximately constant through the whole breeding season, and the female sample was divided chronologically into groups of about 20±2 hares. The group collected from March 25-April 10 contained 20 percent pregnant animals, April 11-29, 81 percent pregnant; April 30-May 7, 63 percent pregnant; May 8-31, 70-80 percent pregnant; June 1-July 15, 50-60 percent pregnant; and July 16-31, 20 percent pregnant: Green and Evans assumed the gestation period to be 36 days (Grange, 1932) and the preimplantation period to be 6 days, leaving a period of only 30 days when the embryos could be macroscopically recognized. During the entire breeding season, Green and Evans calculated 70 days of recognizable pregnancy, which, when divided by the number of days of recognizable pregnancy per gestation period (30) produced an estimated average of 2.35 litters per female per season. Green and Evans used these data with the average litter size and the population density to estimate the number of young hares produced per year at Lake Alexander, Minnesota. Similar calculations for other parts of the snowshoe hares' range are seen in Table 3.

Keith et al. (1966) noted on captive hares that the species is physiologically capable of producing four litters per year. Data on Table 3 indicate that some individuals realize this potential in the wild, except in the far north. Evidence for a fifth litter being conceived on occasion was presented by Keith et al. (1966) and Criddle (1938). Table 3 indicates a tendency for the average number of litters per year and the average total annual production per female to be highest in central sections of the range, and lower both to the north and south.

Tiemeier (1965) cited records of reproductively active juvenile male jackrabbits in Kansas, and Bronson and Tiemeier (1958) noted one indicent of a juvenile female resorbing early stage embryos in late August in the same species in Kansas. Flux (1967) noted that juvenile breeding in European hares probably does not occur in Europe, but a high proportion of first litter females in New Zealand bred later in the summer of their birth. He attributed this to the milder New Zealand winter, and consequent higher survival of first litter young. Only one record of a female snowshoe hare breeding the summer of its birth exists in the literature (Keith and Meslow, 1967). It must be assumed that this is a very rare occurrence, and for all practical purposes juvenile breeding in snowshoe hares is nonexistent.

6. Prenatal Mortality

(a) Preimplantation Loss

Estimates of ova loss between ovulation and implantation (implantation occurs at about seven days in snowshoe hares; Keith, 1965a) are based on the difference between counts of corpora lutea and implantation sites. Since corpora lutea are not all clearly visible by external examination, especially in fixed ovaries, Newson (1964) recommended sectioning the ovaries to about 1 mm thickness. She found Graafian follicles to be 1-2 mm in diameter. Corpora lutea reached a maximum diameter of about 5 mm in mid-pregnancy thereafter decreasing in size only slightly before parturition. Flux (1967) and Lechlietner (1959) found similar size changes in the European hare in New Zealand and jackrabbits in California. Raczynski (1964) noted no significant size change in corpora lutea throughout pregnancy in European hares of Poland.

Newson observed that corpora lutea were usually visible in snowshoe hare ovaries up to four weeks after parturition, but disappeared quickly as the next litter approached full term. At the end of the breeding season corpora lutea disappeared more gradually. Keith (pers. comm.) also found that corpora lutea persisted for some time after parturition. Newson used counts of both new and old corpora lutea where females were less than 28 days pregnant with the new litter in estimating ovulation rates. The snowshoe hare is similar to the jackrabbit (Lechleitner, 1959) and the European hare (Flux, 1965) in the persistence of old corpora lutea into the next pregnancy. In contrast, the European rabbit loses corpora lutea within a few days of parturition (Brambell, 1944).

Atretic and active corpora lutea may be present together in an ovary, and the failure to recognize and atretic follicle could lead to overestimation of the ovulation rate. Halliday (1959) observed that atretic follicles in European rabbit were characterized by small size and lack of a rupture point. Newson (1964) and Ecke (1955) found that atretic follicles were similarly characterized in snowshoe hares and cottontail rabbits had little difficulty in distinguishing them. Newson found atretic follicles to be present in 31 pregnant hares (7 percent) and represented 3 percent of all corpora lutea.

Newson found that preimplantation loss in snowshoe hares where some of the ova had survived to implant was 6 percent (4.5 and 7.3 in two different populations in Ontario). Keith (1965a) found such losses to be 9 percent, with no variation in yearly levels from 1961-64. However, Keith found that loss in first litters was 15 percent, and in subsequent litters 6 percent. Dodds (1960) found preimplantation losses in females where some ova survived to implant to be 9 percent in Newfoundland. Such losses were estimated at between 7 and 9 percent of ova shed in jackrabbits (Lechleitner, 1959 and Tiemeier, 1965) and cottontails (Conaway and Wight, 1962).

In the European hare in New Zealand, Flux (1967) found 3 of 87 females (4.6 percent) with large corpora lutea which seemed to be regressing and he considered these to be cases of pseudopregnancy. Lechleitner (1959) concluded that pseudopregnancy lasted about twice as long as the regular preimplantation period, thus Flux estimated a pseudopregnancy rate of 2.3 percent of pregnancies. In 407 litters in which some ova survived to implant Flux found a preimplantation loss of 28.6 percent of ova shed. Thus, total preimplantation loss in this study was estimated to be 30.9 percent of ova shed. Raczynski (1964) found that preimplantation loss in European hares of Poland was highest at the beginning and the middle of the breeding season (32-45 percent in January and February, and 24 percent in June).

Investigations on the wild rabbit in England (Brambell and Mills, 1947) showed that preimplantation loss of whole litters was as high as 9.5 percent of ova shed, and loss of some ova in a litter was 36.5 percent, giving a total loss of ova shed of 46 percent. Brambell and Mills observed that loss of entire litters before implantation was highest at the beginning and end and lowest at the height of the breeding season. There was no detectable seasonal variation of loss in litters in which some embryos survived.

(b) Postimplantation Loss

Estimation of postimplantation mortality is based upon the difference between counts of implantation sites and living embryos. These estimates will be biased if implantation site counts are not accurate. Newson (1964) noted in snowshoe hares that there was no evidence of a decrease in mean number of sites as pregnancy proceeded, indicating that even sites of early resorptions remained visible throughout pregnancy. In studies of captive European rabbits, which included laparotomies at several stages during pregnancy, Adams (1960) concluded that only in cases where mortality occurred immediately after implantation would the implantation sites have disappeared near full term (day 28). Loss occurring soon after implantation to day 17 was represented by atrophic placentae, and loss after day 17 resulted in dead foetuses being present at day 28.

In cottontail rabbits Lord (1961b) and Evans et al. (1965) estimated postimplantation mortality to be very low. Lord found 0 to 8 percent embryo mortality, and Evans et al. found 5.2 percent of embryos in 13.9 percent of litters died before parturition. Both authors remarked that total litter resorption was lacking or very infrequent in their studies, thus they were not considering it in their estimates. Evans et al. observed partial litter resorption in 24.7 percent of first pregnancies of the season and in only 8.5 percent of subsequent litters. These estimates of postimplantation mortality seem very low but in none is complete litter loss considered.

Conaway et al. (1960) documented a situation within a swamp rabbit population in Missouri after a flood forced all animals together on a small area of high ground. The females were in the midst of bearing the first litter of the season. Partial litter resorption rates remained relatively constant at 10 to 20 percent of ova shed before and after the flood occurred. Total litter resorption was 70 percent of ova shed in the first litter, and 46 percent in ensuing litters that season. Stress produced by the flooding and consequent crowding seems to have played a very significant part here, mainly through increased total litter resorption.

High mortality rates in postimplantation stages have been found in European rabbit. Brambell and Mills (1948) estimated that 35 percent of litters are lost "in toto", with litter resorption concentrated in early pregnancy. The percentage of embryos being resorbed was 3.4 from 7-10 days, 24.1 from 11-15 days, 6.3 from 16-20 days, 2.2 from 21-25 days and 1.2 from 26-32 days. McIlwaine (1962) found resorption occurring in 53 percent of litters, involving 18 percent of ova shed, with the greatest loss occurring in the first 20 days of pregnancy.

Brambell (1948) observed 1.0 percent to 3.5 percent of embryos lost in surviving litters.

In jackrabbits, Bronson and Tiemeier (1958) observed total litter resorption in 8 percent of litters implanted, none of which was older than half-term. Partial and total resorption occurred in 15 percent of all litters, involving 8 percent of all embryos. Bronson and Tiemeier also reported an abnormally high mortality rate following a three day blizzard in March, 1957, when 6 of 17 litters were in the process of being resorbed or aborted. Tiemeier (1965) reported a ratio of 219 litters in early pregnancy to 185 half-term or older (1/0.89), indicating 11 percent loss of entire litters. Of 44 litters in early stages of partial resorption, Tiemeier found the size at death exceeded 40 mm in 15 litters while in the remaining 29, embryos were shorter than 40 mm (approximate measurement for half-term embryo). Resorption was occurring in 3.4 percent of the less than half-term embryos and 1.7 percent of the half-term or older embryos, giving a total partial litter resorption rate of 5.1 percent of embryos.

European hares in Poland (Raczynski, 1964) undergo very heavy postimplantation mortality at the start of the breeding season with a second intensification at mid-season. In January litters, 80 percent of implanted embryos were being resorbed. The level fell to 6-10 percent from February to April, rose to 44 and 47 percent in May and June and was reduced again in July. Resorption of entire litters in New Zealand European hares was estimated (Flux, 1967) for the entire season by comparing the numbers of litters younger (212) and older (181) than half-term, indicating total litter loss of 14.6 percent of all litters, or 14.3 percent of ova shed. Nine percent of ova shed were lost by partial litter resorption.

Keith (1965a) found that two percent of embryos were being resorbed in Alberta snowshoe hares, this presumably being a figure for partial litter resorption. Newson (1964) estimated 20 percent of whole litters lost in an Ontario population of hares, with the highest mortality between 11 and 15 days gestation. Postimplantation losses increased throughout the season, with 4.1 percent of litters showing partial loss in April, 13.0 percent in May and 15.8 percent in June.

(c) Total Prenatal Mortality

Brambell (1948) estimated a total loss of ova shed in the European rabbit of at least 43.3 percent, of which 10.2 percent is lost before implantation and most of the rest lost before half-term gestation. Expressed another way, 35.7 percent of ova shed are lost in litters which do not survive, and 7.6 percent lost from litters which do survive.

Tiemeier (1965) estimated total prenatal loss in jackrabbits at 14.5 percent of ova shed (9.4 percent lost prior to and 5.1 percent lost after implantation), while Lechleitner (1959) estimated 47.4 percent loss of ova on the same species.

Flux (1967) estimated a total mortality of 47.5 percent of the ova shed, 16.6 percent being loss of entire litters (2.3 percent preand 14.3 percent postimplant) and 30.9 percent being partial litter loss (21.9 percent pre- and 9.0 percent postimplant) in a European hare population in New Zealand. The Polish study of European hares (Raczynski, 1964) indicated that 90 percent of ova shed were lost in the January pregnancies, with more than half being lost at the second mortality intensification in May and June.

Newson's (1964) snowshoe hare data show a total loss of ova of about nine percent, with six percent occurring before implantation and three percent after. Keith's (1965a) study showed slightly more than ten percent total prenatal mortality of ova ovulated with pre-implantation losses of about nine percent and postimplantation loss of embryos at about two percent.

The estimates of total prenatal mortality given here vary widely. Lechleitner (1959) and Brambell (1967) both found postimplantation loss of whole litters to be a very important mortality factor. This is difficult to estimate, and several of the above authors have not tried (Newson 1964, Keith 1965a and Tiemeier 1965), while the others (Brambell 1948, Lechleitner 1959, Raczynski 1964 and Flux 1967) attempted to do so. Much of the disparity between the different estimates may be accounted for in this way.

7. Reproductive Aberrations

(a) Polyovulation

In the European hare of New Zealand Flux (1967) found this abnormality in 3 of 320 pregnancies (less than one percent), indicating the occurrence of biovular follicles. Others may have been masked by prenatal mortality. In the same species in Europe, Raczynski (1964) found only two cases, while Bloch and Strauss (1958) found only one case. In extensive collections of black-tailed jackrabbits in Kansas, Bronson and Tiemeier (1958) found only one irregularity which they concluded was caused by either polyovulation or transmigration of ova. Allen et al. (1946) estimated that in European rabbits only 0.23 percent of ovulations produce two ova, while Newson (1964) found six cases in the snowshoe hare, five cases of biovular follicles and one case of triovular follicle.

(b) Transmigration of Ova

Flux (1967) found this phenomenon in 4 of 320 (1.25 percent) pregnant European hares examined in New Zealand, and Raczynski (1964) observed only one case in the same species in Poland. Boyd, Hamilton and Hammond (1944) and Brambell (1948) stated that transperitoneal migration of ova does not occur in rabbits, but Allen et al. (1946) found it in two percent of the litters studied, affecting 0.37 percent of ova in wild European rabbits. Newson (1964) recorded two definite cases of this abnormality in snowshoe hares.

(c) Superfetation

No instances of new implantations occuring while embryos are developing were recorded by Raczynski (1964) in European hares or Bronson and Tiemeier (1958) in jackrabbits. Raczynski concluded that this was of very limited significance in hare reproduction.

(d) Asymmetrical Testes

Flux (1967) observed only one male European rabbit of 636 collected (0.16 percent) which had one small testis (0.5 g) and one large testis (15.0 g). He suggested that this may have been a case of complementary growth, as the larger testis was heavier than any other recorded.

(e) Ectopic Pregnancy

This phenomenon was again recorded only in the European hare where Flux recorded two of 428 pregnant females with one and two embryos loose in the abdominal cavity. The females were otherwise healthy and one had healthy embryos in the uterus.

(f) Unequal Distribution of Embryos in the Uterus

Raczynski (1964) found an even distribution of embryos between the horns of the uterus through the whole season in Polish European hares. A total of 107 embryos were found in the right horn, and 103 in the left horn, although considerable differences were found between different months (March, right 22/left 11, July 10/19). Racsynski (1964) concluded that embryonic mortality did not seem important in this distribution. Studying the same species in Yugoslavia, Valentincic (1956) found that a great majority of the 33 females examined were gravid in the left horn. Several investigations of jackrabbits have indicated that the left horn is more often gravid than the right (Bronson and Tiemeier, 1958, left horn 137 embryos, right horn 103 embryos; Tiemeier

1965, left horn 602 embryos, right horn 535 embryos). Asdell (1964) claimed this to be characteristic of many mammals.

Flux (1967) was able to accurately count corpora lutea from the present and previous pregnancies of 157 female European hares. Of these, 22 (14 percent) had shed most ova from the same ovary both times, 80 (51 percent) had shed more ova from the opposite ovary each time, and the remaining 55 (35 percent) had either the old or new corpora lutea evenly divided. This indicated a definite and significant tendency for ova to be shed by alternate ovaries, and hence for pregnancies to occupy the uterine horns alternately.

(g) Pseudopregnancy

The condition of pseudopregnancy can arise in several ways. If ovulation is induced in a female and fertilization of her released ova does not occur, then the female may continue through a period of pseudopregnancy before ovulation occurs again. Some females which lose the entire litter of fertilized ova before implantation may also be classed as pseudopregnant for a period after the loss. Lechleitner (1959) estimated this period to last about twice as long as the regular preimplantation period in jackrabbits. Indentification of pseudopregnancy is difficult and somewhat subjective, but involves corpora lutea which appear larger than those of the regular preimplantation stage, and which may appear to be in the process of regressing.

Wight and Conaway (1962), in five years of extensive collecting of cottontails, identified no cases of pseudopregnancy, and concluded it to be very rare. Flux (1967) estimated pseudopregnancy occurred in 2.3 percent of pregnancies of European hares in New Zealand, and Bronson and Tiemeier (1958) found no cases in Kansas jackrabbits. In snowshoe hares, pseudopregnancies were estimated by Newson (1964) to represent less than two percent of all litters. The cases found by Newson included two females whose uteri were occluded by the incomplete resorption of a previous litter, and at least three females caught in late July and August which were potential fourth litters. Some pseudopregnancies occurred at the beginning of the breeding season in Newson's study, as in April, 1961, when two pregnant, non-lactating, females were collected which had older corpora lutea as well as current ones. These must have represented either pseudopregnancies or total litter resorption.

8. Factors Affecting Reproductive Parameters and Survival

(a) Seasonal Variations

The proportion of pregnant adult female hares apparently varies quite significantly through the breeding season. French et al. (1965) found a season total of 56 percent of adult jackrabbits in Idaho were pregnant, but the greatest proportion (up to 100 percent) were pregnant in the early part of the season (February-April), after which the proportion fell to the end of the season. In European hares, Raczynski (1964) found a similar trend, with almost 100 percent pregnancy from March to June and a decline to 79 percent in August and 17 percent in September.

Green and Evans (1940c) found distinct seasonal fluctuations in the proportions of snowshoe hares visibly pregnant in Minnesota; March 25-April 10 = 20%, April 11-29 = 81%, April 30-May 7 = 63%, May 8-31 = 70-80%, June 1-July 15 = 50-60%, and July 15-31 = 20%. Keith (1965a) and Newson (1964) found similar seasonal variations in Alberta and Ontario snowshoe hares.

There seems to be a definite tendency for ovulation rates and litter sizes to increase as the breeding season progresses. McIlwaine (1962) found this to be true in European rabbits in New Zealand, the ovulation rate rising from a low of 4.69 in May to a maximum of 8.02 in October, with a corresponding increase in litter size from 3.82 to 6.73 for the period 1952-59. In black-tailed jackrabbits of Kansas, Tiemeier (1965) also found great fluctuations in litter size, from a low of 1.0 in January to a maximum of 4.2 in May and a gradual decrease to the end of the season. Bronson and Tiemeier (1958) in Kansas and French et al. (1965) found similar fluctuations in black-tailed jackrabbit populations.

The European hare showed this same pattern of seasonal variation. In New Zealand the ovulation rate rose from a low of 1.0 in June to a peak of 3.8 in November with a slight decline to the end of the season. A similar pattern was found in Poland (Raczynski, 1964) except the Polish peak ovulation rate was higher, exceeding four in April, May and June.

Rowan and Keith (1956) noted a distinct tendency for the litter size of snowshoe hares to increase through the season. Bookhout (1965a) agreed with this and showed an increase in litter size from 2.20 in May to 2.91 in July, while Newson (1964) noted an increase in ovulation rate from 2 in April to 3 or 4 in May and a decrease to 3 in June and July.

Prenatal mortality also varies seasonally. Myers and Poole (1962) in New Zealand and Brambell and Mills (1948) in England both noted that mortality was greater at the beginning and end than at the middle of the breeding season of the European rabbit. Evans et al. (1965) noted that resorption was most common in the early part of the season for cottontails, with 25 percent of litters being affected, while only 8.5 percent of later litters were affected. Mortality in the European hare also appears to be concentrated at the beginning of the season, with a lesser high at the end, and a low at the peak (Kolosov, 1941—Russia; Raczynski, 1964—Poland; and Flux, 1967—New Zealand). In contrast to this, Newson (1964) found that litter resorption in snowshoe hare increased as the season progressed, rising from a low of 4.1 percent of litters affected in April to a high of 15.8 percent in June.

(b) Annual Variation and Effect of Population Density

Many investigators have simply noted that the parameters of reproduction vary between years, but very thorough investigation of all variables is needed in understanding why these variations occur. For example, McIlwaine (1962) noted annual variation of as much as four weeks in the onset of breeding, and annual variation in the proportions of juvenile and adult rabbits pregnant in New Zealand populations of the European rabbit, but did not investigate reasons for these variations. Myers and Poole (1962) noted, with confined populations of the same species in Australia, that fecundity decreased with increases in density through an increase in the resorption rate and an apparent suppression of estrus behavior. In Britain the prenatal mortality of this species has been noted as varying between years and areas (Brambell and Mills, 1948).

French et al. (1965) studied a jackrabbit population in Idaho during a period of increase from 1956 to a high in 1959, and a sharp decrease during 1960. They found that the length of breeding season varied inversely to population density, being 135, 130, 124, 120 and 132 days long in 1956 through 1960. Similar relationships were found between density and yearly figures for production of young per female (2.80, 2,32, 1.76, 1.20, and 1.70 for 1956-60) and prevalence of pregnancy (77%, 59.5%, 53%, 43.5%, and 49%, 1956-60). French et al. (1965) concluded that reproduction in Idaho jackrabbits is controlled in a density-dependent fashion through the frequency of pregnancy and litter size. These two factors act independently on the population, and it was suspected that delayed onset of breeding was compensated for by a greater production of young later in the season.

MacFarlane (1905) suggested that litter size of snowshoe hares varied from year to year, with large litters in years of population increase and small litters in years of decline. Preble (1908) and Elton (1924) supported this view, but none presented sufficient data to verify the point. Aldous (1937) studied hare populations in Minnesota during years of increase in 1931 and 1932, a peak in 1933, and a decline in 1934 and 1935. He noted a gradual decline in litter size from 4.8 in 1931 to 2.65 in 1935, with this decline starting several years before the peak year. Bookhout (1965b) found little yearly variation of litter size in Michigan hares, but his average litter size never exceeded 3.0 in any year, and the greatest change in average litter size between years was 1.0 young. Trapp (1962) observed that litter size may vary with changes in population density in Alaskan hares, and Dodds (1965) presented good evidence to support this relationship in Newfoundland. Criddle (1938), Green and Evans (1940c), Severaid (1942) and Adams (1959) found no correlation between litter size and cyclic fluctuations in hare density.

Conaway et al. (1960) found an increase in resorption of swamp rabbit litters with increasing population densities due to flooding. Mykytowycz (1960) and Christian and Lemunyan (1958) reached similar conclusions with experimental colonies of European rabbits and house mice. This effect was not found in a study of a population decline in Ontario snowshoe hares (Newson, 1964). Newson concluded that juvenile mortality was the most important factor in a population decline, concurring with the conclusions of Green and Evans (1940c) for hares, and Chitty (1952) for Microtus.

Rowan and Keith (1956) suggested that reduction in litter size accompanies cyclic declines of snowshoe hares, and their four years' data (1949-52) around the peak year of 1950 in Alberta support this suggestion. An extensive study in Alberta (1961-64) including a peak year in 1961 (Keith, 1965a) showed a great decrease in the mean number of young per female per year during the two years of rapid population decline 1962 and 1963 (13.0 young, 8.6 young, 5.9 young, 11.9 young for 1961-64). This reduced production of young was due to a combination of variables, including ovulation rate, incidence of pregnancy, and mean number of litters per female (mainly the influence of a fourth litter grouping in 1961 and 1964). Keith found a constant rate of prenatal mortality from year to year, but juvenile and adult mortality changed greatly between years. Adult mortality was found to be less than 52 percent annually before the decline, and 83 percent during the decline. Juvenile mortality was lowest in 1961 and highest in 1962 and 1963, with annual rates as high as 99 percent. The cyclic decline in Alberta was caused by an approximate halving of the reproductive rate, a doubling of the adult mortality rate, and an increase of first year mortality to 99 percent.

(c) Geographic Variation

Lord (1960) observed that many species of non-hibernating lagomorphs and rodents show an increase in litter size with increasing latitude, and presented data to support this contention in cottontail rabbits. Barkalow (1962) supported this thesis with data on the swamp rabbit. Evans et al. (1965) found no correlation between onset of cottontail breeding and latitude, but their litter sizes tended to increase from south to north. Lord concluded that the selective factor in this situation must be severity of the winter, and associated winter mortality.

Investigators studying black-tailed jackrabbits have found considerable variation in the length of the breeding season and average litter size with latitude. In Arizona the jackrabbit breeds for a period of at least ten months (Vorhies and Taylor, 1933), in California the season is 242 days (Lechleitner, 1959), in Kansas it lasts 220 days (Bronson and Tiemeier, 1958), and in Idaho 128 days (French et al., 1965). The overall average litter size increases from a low in Arizona of 1.79 (Haskell and Reynolds, 1947) and 2.24 (Vorhies and Taylor, 1933) to 2.3-2.5 in California (Lechleitner, 1959), 2.6 in Kansas (Bronson and Tiemeier, 1958) and 3.35 in Idaho (French et al., 1965). Bronson and Tiemeier (1958) commented, however, that the larger litter size about compensated for the smaller number of litters, and the total production figures from these areas were not greatly different.

Flux (1967) made a comparison of mean litter size of the European hare and found a close correlation between litter size and mean annual temperatures, or latitudes. Litter sizes varied from a low of 2.2 young in the north island of New Zealand to a high of 2.8 in Canada.

Keith et al. (1966) summarized the reproductive characteristics of the snowshoe hare over its principal geographic range. The breeding season of this species has been shown to be remarkably similar in onset, duration and termination over its whole range (Table 2). The data in Table 3 show a distinct increase in litter size from south to north, and Keith et al. demonstrated that these differences are genetically determined. Table 3 also shows that the average number of young produced per female per year are greatest at the intermediate latitudes. Factors governing these variations in production of young are complex, and need a fuller explanation.

(d) Climatic Effects

Lyman (1943) observed that the onset of breeding is governed exogenously by the increase in daylength and endogenously by a basic rhythm, and he demonstrated that by altering the duration of illumination he could greatly modify both the sexual and moulting cycles of snowshoe hares. Bissonette (1938) and Bissonette and Csech (1939) induced modifications in the cottontail sexual cycle by altering the photoperiod.

Severe weather has also been known to influence the onset of cottontail breeding. Wight and Conaway (1961) recorded a delay of four weeks in the onset of Missouri cottontail breeding caused by a series of heavy snowstorms at the time of normal first conceptions. In the Missouri incident of swamp rabbits being concentrated on high ground by flood waters, Conaway et al. (1960) found that ovulation rate and partial resorption rates were not affected, but total litter resorption or abortion caused mortality in 40-60 percent of the ova shed.

Bronson and Tiemeier (1958) cited an example of abnormally high total litter mortality in black-tailed jackrabbits of Kansas following a spring blizzard, when litters in six of 17 pregnant females were undergoing resorption.

Stieve (1952), Siivonen (1956) and Raczynski (1964) suggested that the European hare breeds earlier in mild than cold winters. Flux (1967) found a close and significant correlation between the onset of breeding and temperature in this species in New Zealand. Lechleitner (1959) found that the yearly precipitation cycle and vegetation depending on it influenced the onset of reproduction of the black-tailed jackrabbit in California.

Keith (1965a) found that breeding started progressively later from 1961-63 (March 31, April 8, April 14) and was earlier again in 1964 (April 9). He found no correlation between the earliness of breeding and daily temperature, precipitation, sky conditions and snow conditions.

(e) Effects of Age and Physiological Condition

Lord (1961b and 1963) found that the average litter size in cottontails increased with age to at least three years, varying from a low of 4.72 in juveniles to a high of 6.00 in three year old females. The prevalence of pregnancy also varied with age, being 0.31, 0.77, 0.70, and 0.68 for females aged from juvenile to three years. Figures for production of young per female followed a similar pattern (1.46, 4.20, 4.11 and 4.08). Lord found an inverse relationship between the amounts of juvenile and adult breeding.

In a confined population of European rabbits Myers and Poole (1962) found that older females had more and larger litters, and reduced resorption losses than younger females. Myers and Poole found no relationship between length of gestation period and either age of female or size of litter. In wild populations of European rabbit McIlwaine (1962) observed that rabbits aged 10-33 months had the highest ovulation rate, those over 33 months were second, and those less than ten months old had the lowest ovulation rate.

Flux (1967) found in New Zealand populations of European hare that 35 breeding juveniles had a much lower mean number of corpora lutea (1.80), implantation sites (1.64) and healthy embryos (1.50) than adults (2.81, 2.55 and 2.21 respectively). Prenatal mortality rates appeared to be similar in juveniles and adults. Newson (1964) found a distinct tendency in snowshoe hares for ovulation rate to increase with maternal age.

Brambell and Mills (1948) found the loss of entire litters in European rabbits declined steeply with increased maternal body weight, and also noted that mortality of litters was greatest in lactating females. McIlwaine (1962) observed that adult rabbits showed a distinct tendency to increased litter size with increased maternal eviscerated weight. Litter size varied from 5.33 in 1,100 g females to 7.0 in 1,900 g females. Juvenile females showed no such pattern. A similar pattern of ovulation rate:weight was seen in snowshoe hares (Newson, 1964).

X. GROWTH AND DEVELOPMENT OF THE YOUNG

Snowshoe hare young are born fully furred and with open eyes after a gestation period of 37 days (Hall and Kelson, 1957). Weight of young within a few hours of birth can be quite variable. Measurements in the literature have varied from 39.6 to 85.0 mm (Grange, 1932; MacLulich, 1937; Criddle, 1938; Severaid, 1945; Adams, 1959; and Trapp, 1962). Bookhout (1964) maintained a colony of captive snowshoe hares in Michigan and sacrificed 20 pregnant females (a total of 53 young) at various stages of gestation between seven and 34 days. Bookhout used a combination of length, weight and morphological features of embryos to draw up a prenatal growth curve which he felt was accurate to ± one day. Keith (unpublished) used additional data from captive and wildreared hares with that of Bookhout and unpublished material of Joseph Dell (New York State Conservation Department) in the aging of hare embryos. Keith felt these data enabled him to age embryos quite accurately.

Aldous (1937) believed that the period of parental care was short in snowshoe hares. His observations in Minnesota caused him to conclude that the young were completely weaned by one month of age. Grange (1932) observed that a captive second litter was nursed for six weeks to two months, although the young also ate quantities of greens before this time. Severaid (1945) observed in captive hares that young were weaned in 25-28 days, although terminal litters were often nursed up to 56 days.

A number of investigators have published data on the growth rate of young snowshoe hares (Grange, 1932; MacLulich, 1937; Severaid, 1942; Adams, 1959; and O'Farrell, 1960). These growth curves were mostly based on change in body weight. Keith (unpublished) felt that body weight was not sufficient, and used a combination of body weight with length of the hind foot. Keith made extensive measurements of growth rates on captive hares and found marked differences between captive and wild growth rates in body weight, hind foot length and lens weight data. He modified the captive growth curve with data collected from wildreared hares and derived a growth curve based on body weight and hind foot length which was accurate to 90 days of age.

XI. FOOD HABITS

During the spring and summer, with all the succulent vegetation available, snowshoe hares probably have an almost unlimited diet diversification. Some plants have been singled out as important in summer despite this great availability. Criddle (1938), in Manitoba, observed that the Gramineae, including bluegrass, brome, timothy, and the cereal grains were important foods. Members of the Compositae family were also mentioned as being important, including Aster spp., Taraxacum spp. (dandelions), Balsamorhiza spp., and Arnica spp. Leguminosae are also important summer foods, including Medicago spp. (alfalfa), Trifolium spp. (clovers), and Vicia spp. (vetch). Other plants mentioned were Impatiens spp. (jewelweed) of the Aceraceae, Spiraea spp. of the Rosaceae, and Erythronium spp. of the Liliaceae (Grange, 1932; Criddle, 1938; Adams, 1959).

In winter, when the annual forbs die and low bushes become covered with snow, the snowshoe hare is dependent on high bushes and trees, and its diet is much more restricted. Several authors have ranked food species for their importance in the hares-winter diet. Trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*) seem to be the most highly utilized species over wide areas of hare range (Grange, 1932—Wisconsin; Criddle, 1938—Manitoba; Trapp, 1962—Alaska; and Bookhout, 1965a—Michigan). Bookhout mentioned the following species as also being highly utilized by hares: paper and yellow birch (*Betula papyrifera* and *B. alleghaniensis*), white cedar (*Thuja* spp.), sugar maple (*Acer saccharum*), American elm (*Ulmus americana*), jack, red and white pines (*Pinus banksiana*, *P. resinosa* and *P. albicaulis*), black spruce (*Picea mariana*), eastern hemlock (*Tsuga canadensis*), and beaked hazel, (*Corylus cornuta*). Criddle also observed high utilization of beaked hazel, and mentioned the importance of bog birch (*Betula pumila*), bur oak (*Quercus macrocarpa*), wolf willow (*Elaeagnus commutata*) and other willows (*Salex* spp.), hawthorne (*Crataegus* spp.), plum and cherry shrubs (*Prunus* spp.), and most lesser shrubs in Manitoba.

Trapp (1962) also found willows, paper birch and black spruce to be important foods in Alaska, and listed bog bilberry (*Vaccinium uliginosum*), Labrador tea (*Ledum groenlandicum*), rose (*Rosa acicularis*), alder (*Alnus fructicosa*), and balsam poplar (*Populus balsamifera*) as being utilized foods. Adams (1959) observed that douglas fir (*Pseudotsuga taxifolia*) and *Berberis repens* were the most highly utilized foods in Montana, and Dodds (1960) found that birch was the most important food species in Newfoundland.

Criddle (1938) noted that hares rarely ate Manitoba maple (*Acer negundo*), highbush cranberry (*Viburnum trilobum*), Saskatoon-berry (*Amelanchier alnifolia*) or snowberry (*Symphoricarpos albus*). MacLulich (1937) observed that wild and captive hares refused to eat *Clintonia borealis*.

Bookhout (1965a) observed that the mean pellet deposition rate of captive hares in Michigan was 466 per day, with a range of 348-535, and he noted that fewer pellets were produced from the best diets in his feeding trials. Adams (1959) observed reingestion of pellets on four occasions in the wild, and on many occasions with captive animals. The pellet was taken directly from the anus, put into the mouth, chewed and swallowed. Lord (1964) observed that the cottontail rabbit's usual method of digesting its food, since it lacks a rumen, was to reingest certain food pellets to complete their digestion.

MacLulich (1937) reported that hares would eat any kind of frozen flesh, and Trapp (1962) concluded that they would eat meat when it was available as carion. Hardy (1910) reported hares eating dead fish, and Soper (1921), Criddle (1938), and Seton (1953) reported hares eating the flesh of carcasses of all kinds including other hares. Trapp (1962) and MacLulich both reported hares eating sand, sometimes in large quantities. This is a common occurrence in New Brunswick in the breeding season, and seems to be done largely by pregnant hares (Wood and Munro, unpublished).

XII. POPULATION DYNAMICS

1. Sex Ratios

Sex ratios for the snowshoe hare are given in Table 4, with comparative data for black-tailed jackrabbit and European hare in Table 5. Most data in these two tables do not differ significantly from equality. O'Farrell's (1960) ratio for April, 1960, of 75 percent males may be explained by the greater activity of males in the breeding season, and was not a reflection of the true sex ratio. Rowan and Keith (1956) found a significant change from a scarcity to a preponderance of males in a year of peak density and years of decline. However, Keith (1965a) found no divergence from a 1:1 ratio in either adult or juvenile ratios in extensive work from 1961-64.

Flux (1967) found significant differential mortality in male European hares in New Zealand which is reflected in his data in Table 5. In litters which suffered postimplantation mortality the proportion of males was 56.8 percent (n = 81 embryos), while in litters which suffered no such mortality, the proportion of males was 53.8 percent (n = 132 embryos). Raczynski (1964) found 55.1 percent males (n = 49 embryos) in litters showing embryonic mortality, and 50 percent males (n = 96 embryos) in litters showing no mortality in Poland.

2. Mortality

Eberhardt et al. (1963) observed that rabbits have an extremely high mortality rate which is a necessary corollary to a high reproductive rate. Green and Evans (1940b) observed annual adult mortality of the snowshoe hare to average about 70 percent per annum over the period 1932-38, although in the winter of 1937-38 it increased to the level of 97 percent, a rise of 50 percent over the levels of the previous winter, and returned to near normal in 1938-39. Green and Evans concluded that adult mortality remained relatively constant through all years of the study, but that great yearly variations were seen among juvenile mortality rates (Table 4).

Keith (1965a) found that adult mortality did vary between years, (Table 6). Adams (1959) found adult mortality in Montana to be 78 percent during a population decline, but studied no years of increase for comparison. Although Green and Evans (1940b) concluded there was no change in adult mortality between years of increase and decline, Keith cited the increase in adult mortality to 97 percent in 1937-38 as evidence to the contrary.

Green and Evans (1940b) concluded that changes in juvenile mortality alone were responsible for the population cycle which they had studied (Table 6). Keith (1965a) agreed that juvenile mortality changed between years of population increase and decline, noting from age ratios a high in juvenile mortality in 1962 which was 4.5 times higher than 1961 (the year of peak density). Keith observed that the mortality rate from the time of trapping (about 52 days of age) to January was relatively constant each year, and the differences in mortality occurred chiefly between birth and 52 days of age (Table 6). Dodds (1965) also noted a differential mortality of juveniles, citing a change in the mean proportion of juveniles from 89.1 percent in September samples to about 67 percent in October-December samples. Dodds concluded that the population decline from the 1960 peak in Newfoundland was caused by increased juvenile mortality. Tiemeier (1965), studying the black-tailed jackrabbit in Kansas, found variation from 35-85 percent in juvenile mortality from birth to autumn, with a mean juvenile mortality rate of 63 percent for this period. In cottontails, Lord (1961a) found a 75 percent mortality rate in the first four months of life.

3. Predation and Disease

Saunders (1963) reported that the Newfoundland lynx consumed an estimated 200 hares per year. Dodds (1965) observed that high lynx populations were generally correlated with high hare populations, but that hare populations continued to increase despite the maximum predation pressure exerted by the high lynx populations. Dodds concluded that predation by lynx was probably not a major factor involved in the hare decline.

MacLulich (1937) observed seven recently captured and confined hares die in convulsions from what he termed "shock disease". Adams (1959) observed the same phenomenon in five percent of adult hares and 25 percent of juveniles which he handled in Montana. Adams attributed this "trap sickness" to hypoglycemia. O'Farrell (1960 and 1965) observed death by hypoglycemic "shock" in 20 juveniles and no adults. These juveniles all weighed 200-300 grams, and all deaths occurred in June, July and August. Keith (pers. comm.) studied this "shock" phenomenon in Alberta, and observed that it was characterized by a drastic decline in the level of blood sugar. Wood (unpublished) noted that mortality of this type in New Brunswick occurred mainly in the summer and early fall, and mostly in juvenile hares.

4. Parasites

Table 7 summarizes data on common snowshoe hare parasites from various parts of the range. Bookhout (1965a) found that young snowshoe hares showed first incidence of both endo- and ectoparasites at about four weeks of age, and that parasite burdens could be considerable, even in the youngest hares. Some investigators have concluded that immature hares are more susceptible to parasitism than adults, but Erickson (1944) found greater infections of most species of helminths in adult hares. Bookhout's (1965a) data showed that massive infestations of young hares are possible, and he concluded that such loads may have more drastic effects on young hares.

Erickson (1944) believed that Obeliscoides, Trichostrongylus, Nematodirus, Passalurus, Protostrongylus and Taenia were significant factors in hare mortality. MacLulich (1937), and Dodds and Mackiewicz (1961) believed that Obelisoides was an important factor in hare declines. Bookhout (1965a) found little evidence that ectoparasites were of any pathological significance. Green and Schillinger (1935 and 1936) stated conclusively that ticks were primary vectors of tularemia, and concluded that the disease had an important role in the hare decline between 1933 and 1934. Bookhout observed that the effects of mites and fleas in his study were negligible.

Bookhout (1965a) concluded that lungworms and stomach worms almost certainly damaged the well-being of the host when infection was heavy, and Multiceps blisters showed indication of mechanical damage in some cases. Erickson (1944) pointed out that extensive parasitism of wild animals may not be accompanied by demonstratable pathological conditions, but that this afforded no basis for believing the parasites to be harmless. Bookhout concluded that the most subtle influences of parasitism may be inconspicuous, but nonetheless of paramount importance to the infected host.

5. Population Cycles

Hairston et al. (1960) sumarized evidence to show that populations of herbivors are seldom food limited and most often predator limited. They concluded that herbivors are not likely to compete for common resources, and thus are not limited by resources in the classical density-dependent fashion. Hairston et al. dismissed population control by the vagarities of the weather, which was substantiated in studies of snowshoe hare (Keith et al., 1966) and black-tailed jackrabbit (French et al., 1965).

Christian (1956) produced evidence that crowding alters the reproduction of young mice, thus implicating social-psychological factors in population control. The mechanism was not clear, but was evidently density-dependent. French et al. (1965) found changing production of young in a black-tailed jackrabbit population to be density-dependent. In their study food and predation were not limiting, and disease and parasites did not seem to effect the well-being of the population. French et al. concluded that a social-psychological factor or some other manifestation in intraspecific competition was limiting the jackrabbit population in a density-dependent manner.

The snowshoe hare is well known for the distinct and regular cyclic fluctuations in population densities it displays. Keith (1963) reviewed data from six Canadian provinces and the Northwest Territories and calculated the average time between cyclic highs as 8.3 years and lows as 8.9 years. These cyclic fluctuations can show amazing extremes. Estimates have ranged from as low as one hare per square mile to as high as 30,000 hares per square mile (Keith, 1963). The causes behind this regular and incredible cyclic pattern remain one of the biggest mysteries in ecology.

Criddle (1938) saw no evidence of variation in birth rates between years of increasing and decreasing abundance, and attributed the increases in density to an absence of ticks and disease. MacLulich (1937) observed that reproductive output (mainly litter size) changed in relation to the change in population trend, but considered that this alone could not account for the cycle. Green and Evans (1940c) denied a variation in reproductive output with population trend, and accounted for cycles by changes in juvenile survival rates. Dodds (1965) concluded that neither the decline in reproductive rate nor the disproportionate sex ratio favoring males which he observed accounted fully for the sharp population decline in Newfoundland in 1960. He concluded the decline was caused by a great decrease in juvenile survival.

Keith (1965a) conducted a most extensive study into the problems of this cyclic species and concluded that the fluctuations are the combined result of a variable reproductive rate, including litter size, number of litters, and incidence of pregnancy, variable adult mortality; and variable juvenile mortality.

LOCATION AND DESCRIPTION OF AREA

The major portions of this study will be conducted on a 500 acre study area at the Acadia Forest Experiment Station near Fredericton in central New Brunswick. Complementary data relating to certain aspects of snowshoe hare ecology will be gathered in other areas of New Brunswick, Nova Scotia, and Prince Edward Island. Work effort will be divided approximately 75% in central New Brunswick, and 25% in the other areas. The study areas will be further defined at a later date when logistical problems related to the gathering of data have been more fully investigated.

METHODS

This study has been designed in three basic stages, as follows:

1. Live Trapping Program

An extensive program of live trapping is planned for central New Brunswick to yield data on population density, reproduction, age and sex ratios, natality, mortality, movements, growth of young and body condition. Population density will be estimated by mark-recapture techniques in the spring before young have become active, and again in the autumn after reproduction has ceased and all young are of trapable age. Live trapping will also be carried on periodically throughout the breeding season.

2. Collection and Post-mortem Examination of Specimens

Periodic sampling of hare populations will be made throughout the year, with particular emphasis on taking specimens during the breeding season. Carcasses will be thoroughly examined for data relating to reproduction, growth of young, body conditions, age and sex composition, parasites and disease. Considerable effort will be expended on taking a large sample each year in central New Brunswick in order to study in detail the above listed parameters. Collections will also be made in other parts of New Brunswick, Prince Edward Island and Nova Scotia for the purpose of studying reginal variations in reproductive patterns in the Maritime provinces.

3. Food Habits and Habitat Preferences

A series of permanent quarter-milacre plots will be established on the study area at Acadia Forest Experiment Station. Periodic collection of hare fecal pellets from these plots will yield data on habitat utilization by hares. These plots will also form the basis for study of winter food habits of hares and ungulates each spring, and analysis of vegetative composition of the study area. Habitat utilization in winter months will be studied by means of track counts on a number of transects in the study area.

More extensive investigations of hare damage to the regeneration of commercially valuable tree species in central New Brunswick are also planned. This phase of the work will be integrated with other studies of browsing and forage production being carried out under Project M2-5-3. Reported incidents of extensive hare damage to habitat and especially to forestry values will be investigated whenever possible.

MATERIALS AND EQUIPMENT NEEDED

1	Station wagon equipped for all-weather use.
1	Motorized toboggan of the "ski-doo" variety.
150	Live traps - National Live Trap Co., Tomahawk, Wisconsin.
3 prs.	Snowshoes.
1	20 guage/.22 rifle collecting gun.
1	Triple beam balance acc. to 0.1 gm., cap. 2,500 gm.
1	Analytical balance, acc. to 0.1 mg.
1	Drying oven.
1	Refirgerator.
1	Freezer.
1	Compound microscope.
1	Binocular dissecting scope.
	Miscellaneous pieces of field and laboratory equipment and chemical supplies.

Note: Most of the major items required are now available at the Fredericton headquarters (C.W.S.), or have been ordered.

PERSONNEL AND COOPERATION REQUIRED

The logistics of this study, as planned, are such that project leader T. J. Wood will need the full-time assistance of a Wildlife Technician, plus a student assistant each summer. It is hoped that complete portions of this study can be contracted to graduate students working for Master's degrees at universities in the region. Mr. Stan Munro, a student of Mr. Bruce Wright, Northeast Wildlife Station, is at present carrying out a study of the reproductive biology of the snowshoe hare for a Master's thesis as part of this project. Mr. Munro will carry out the "Collection and Post-mortem Examination of Specimens" phase of this project in central New Brunswick during the 1968 breeding season.

To facilitate a study of the reproductive biology of the snowshoe hare throughout all of the Maritime provinces, an effort will be made to hire undergraduate students on contract each year in Prince Edward Island and Nova Scotia, whose duties will include the collection and examination of hare carcasses during the breeding season. In this way, regional differences in such factors as onset and cessation of breeding, litter size and litter number will be studied.

DURATION OF THE PROJECT

This study has been designed to last four years. Intensive field work will be carried on throughout the breeding season (February through August) for four years, 1968 through 1971. Less extensive field investigations are also planned for fall and winter periods during the three winters of 1968-69 through 1970-71. A completion report for this project will be prepared and submitted by the fall of 1972. A more complete schedule of these plans must await a decision on the amount of manpower assistance to be made available.

APPENDIX

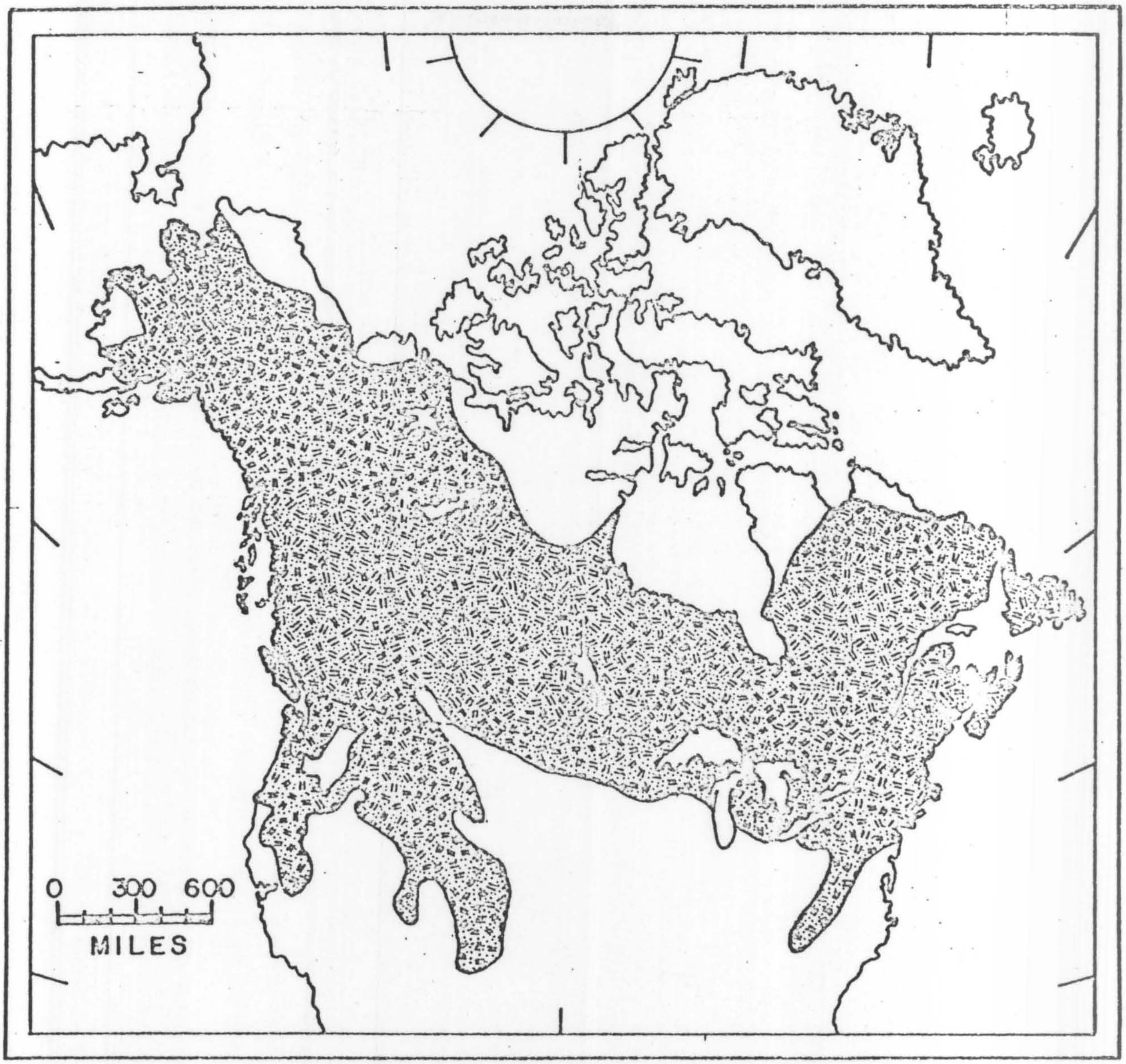

Figure I. Range of the Snowshoe Hare (Hall and Kelson, 1959)

Table 1. Size of Home Range of the Snowshoe Hare

Source	Home Range in Acres				
	Both Sexes	Adults		Juveniles	
		Male	Female	Male	Femal
Seton (1953) bushy areas open woods	20-30 40-60				
Grange (1932 Wisconsin	10				
Keith (1965a) Alberta	5-40				
Adams (1959) Montana		25.2	18.9	12.6	15.3
Bider (1961) Quebec		18.2	7.0		
Bookhout (1965a) Michigan		22.5	17.3		
O'Farrell (1960)* Alaska		14.5	14.4		
Trapp (1962) Alaska		12.1	14.1		

* Data recalculated by Trapp (1962)

Table II. Dates of Conception of the Snowshoe Hare (Keith et al., 1966)

Region, years studied Reference	Dates of Conception First Litter Group		
	Average	Earliest	Latest
Lintereur (unpub.) - 1965 Wisconsin		April 7	
Bookhout (1965b) - 1959-61 Michigan	Ap. 1-15	Ap. 3-10	July 6-30
Aldous (1937) - 1931-35 Minnesota		Mar. 14*	July 26*
Green & Evans (1940c) - 1932-38 Minnesota	Ap. 4-18*		
Newson (1964) - 1959-61 Ontario	Ap. 11-17	Mar. 30-Ap. 3	July 13-26
Adams (1959) - 1953-54 Montana	Mar. 24-Ap. 7	Mar. 13	
Dodds (1965) - 1954-62 Newfoundland		Ap. 4	Aug. 3-4
Criddle (1938) - 1923-35 Manitoba	Mar. 24-Ap. 7*	Mar. 15	Aug. 17*
Hochbaum (unpub.) - 1943 Manitoba	Ap. 4	Mar. 24	
Keith et al. (1966) - 1961-65 Alberta	Mar. 31-Ap. 14	Mar. 27-Ap. 3	June 24-July 2
Rowan & Keith (1956) - 1949-52 and Keith (unpub.) 1956-57 Alberta		Ap. 1	Aug. 15
Tovey (unpub.) - 1955-56 Alaska	Ap. 26-30	Ap. 18	June 30
Trapp (1962) - 1958-61 Alaska	Ap. 8-22*	Ap. 10	June 29

* Dates estimated by Keith et al. (1966) from information in separate papers

Table III.

Reproductive Output of the Snowshoe hare (Keith et al., 1966)

Region, Approx. Latitude, Years studied & Reference	Average Litter Size (embryos)			% pregnancy May-July indicated by:		Litters/adult Female/year		Av. young/adult Female/year
	First Litters	Later Litters	Max.	Embryos	Corpora L. & Embryos	Av.	Max.	
Wisconsin, lat. 45°, 1965 Lintereur (unpub., in Keith et al., 1966)		2.20±.39* (10)	4					
Michigan, lat. 46°, 1959-61 Bookhout (1965a)		2.83± ? (48)	5	60 (60)		2.42	4	6.5
Minnesota, lat. 46°, 1931-35 Aldous (1937)	2.04±.15 (38)	2.79±.04 (194)	7				4	
Minnesota, lat. 46°, 1932-38 Green & Evans (1940 c)	2.40±.11 (45)	3.17±.15 (36)	7	59 (158)		2.35	3	6.8
Ontario, lat. 46°, 1959-61 Newson (1964)	2.38±.05** (225)	3.48±.05** (433)	6		88 (362)		4	6.3
Montana, lat. 48°, 1953-54 Adams (1959)			5	77 (53)		2.94	3	8.2
Ontario, lat. 49°, 1933-35 MacLulich (1937)	2.25±.22 (12)	3.39±.24 (13)	6					

Table III. Cont'd.

Newfoundland, Lat. 49°, 1954-62 Dodds (1965)	2.77± ? (15)	4.23± ? (164)	8	73 (117)	93 (117)	3.20	4	12.2
Manitoba, lat. 50°, 1923-25 Criddle (1938)	2.52±.09 (56)	4.21±.12 (42)	8				5?	
Manitoba, lat. 50°, 1943 Hochbaum (unpub. in Keith et al., 1966)	3.40±.27 (10)							
Manitoba, lat. 51°, 1933 MacLulich (1937)	4.18±.21 (23)							
Alberta, lat. 54°, 1961-65 Keith et al., (1966)	2.71±.13 (45)	4.49±.15 (87)	9	70 (266)		3.15	4	12.8
Alberta, lat. 56°, 1949-52 & 1956-57; Rowan and Keith (1956) & Keith (unpub.)	2.88±.26 (9)	4.06±.14 (63)	7	69 (100)		2.75	5?	10.5
Alaska, lat. 60-65°, 1937 Philip (1939)		4.91±.17 (44)	7					
Alaska, lat. 65°, 1955-56 Tovey (unpub. in Keith et al., 1966)	3.72±.23 (29)	4.33±.13 (88)	7	64 (118)		1.79	3	7.2
Alaska, lat. 65°, 1958-61 Trapp (1962 & unpub. in Keith et al., 1966)		4.63±.50 (8)		57 (78)		1.68	3	7.8

* Confidence limits represent ± S.E. and numbers in parentheses indicate sample sizes.

** Based on Corpora Lutea counts rather than number of live embryos.

Table IV. Snowshoe Hare Sex Ratios

	Total	Adult	Juvenile
Aldous (1937) Minnesota - increasing & peak population densities	54%* (1625)		
Webb (1937) Minnesota - peak population density	53.6% (3930)		
Severaid (1942) - Maine high population		49.3% (219)	54.6% (119)
MacLulich (1937) Ontario	47% (269)		
Dodds (1965) Newfoundland 1954-60	53% (854)	52% (496)	54% (358)
O'Farrell (1960) Alaska - low density mean April 1960	53% (207) 75% (114)		
Trapp (1962) Alaska - low density May 1960 - November 1961		48% (229)	48% (504)
Adams (1959) Montana declining population			58% (101)
Rowan & Keith (1956) Alberta			
1949-50 - peak density	30.3%		
1950-51 - decline	60.6%		
1951-52 - decline	56.9%		

* Expressed as percentage of males
Figures in parentheses are sample sizes

Table V. Sex Ratios of Other Hares

	Total	Juvenile	Embryonic
Black-tailed jack rabbit - Kansas Tiemeier (1965)	50.4%* (2627)		48.5% (262)
European hare - New Zealand Flux (1967)	45%	52%	54.9% (213)
Canada - Reynolds (1952)	52.1% (142)		
Yugoslavia - Valentincic (1950)	52.5% (61)		
Switzerland - Fraguglione (1961)	48.3% (89)		
Poland - Raczynski (1964)	52.1% (764)		51.7% (145)

* Expressed as percentage of Males
Figures in parentheses are sample sizes

Table VI. Mortality Rates in the Snowshoe Hare

	Annual Juvenile Mortality Rate	Monthly Mortality Birth - 52 days	Monthly Mortality Birth - 200 days	Annual Adult Mortality
Green & Evans (1940b) - Minnesota				
increasing 1932	50%			
peak density 1933	77%			
declining 1934-37	71, 82, 88, 92%			70%
increasing 1938	8%			
Adams (1959) Montana				
declining density - 1953, 1954	91%	33%	26%	78%
Keith (1965a) Alberta				
increasing	92%			52%
declining	98-99%	51-55%	35-37%	83%

Table VII. Parasites of the Snowshoe Hare

I. Cestodes (Tapeworms)

Cittotaenia pectinata - adult form scarce in Ontario hares(1), infection 6% Minnesota hares(2)

Taenia pisiformis - Cysticerci larval "bladders" infect: 44% Ontario hares(1)
42% Michigan hares(3)

Multiceps serialis - Coenuri larval "blisters" infect: less than 10% Ontario hares(1)
6% Minnesota hares(2)
8% Michigan hares(3)
0.32% Newfoundland hares(4)
common in Alaskan hares(5)

- Adult tapes--found in 2 adult and 2 juvenile hares in Michigan(3); none found in Newfoundland(4); common in Alaskan hares(5)

II. Nematodes (Roundworms)

Trichuris leporis (whipworm) - found in Ontario,(1) infects: 53% of hares in Michigan(3)
27% in Minnesota(2)

Nematodirus triangularis - found in Ontario hares,(1) infects: 13% Michigan hares(3)
20% Minnesota hares(2)

Protostrongylus leporis - found in Ontario hares(1)

Trichostrongylus calcaratus - found in Ontario hares(1), infects: 86% of Michigan hares(3)
30% of Minnesota-hares(2)

Table VII.-Cont'd.

Obeliscoides cuniculi (Stomach worm) - 100% infection in Ontario hares(1)
96% in Michigan(3)
58% in Newfoundland(4)
Infection spotty in Alaska(5) & (6)

Passalurus ambiguus - Occurred in Ontario(1), infection: 42% in Michigan hares(3)
27% in Minnesota hares(2)

Wellcomia evoluta - identified in one Ontario hare(1)

Synthetocaulus leporis (Lungworm) - occasional occurence in Ontario(1)

Protostrongulus boughtoni - infected: 83% of hares of Western Canada(7)
44% in Michigan(3)
42% in New York(8)
common occurence in Alaska(6)

Dirofilaria scapiceps (Hockworm) - found in 1 hare in Ontario(1), 68% infection rate in Michigan(3), occurred in Alaska(6)

III. External Parasites

Mites
Haemogamasus alaskensis - identified on Ontario hares(1)
Trombicula microti (chigger) - identified on Ontario hares(1)
Cheletiella pasasitivorox - identified on Ontario hares(1)
family Nothridae - adult beetle mite found on one hare in Ontario(1)

Ticks
Haemaphysalis leporis-palustris (rabbit tick) - summer infestation 100% in Ontario(1), Michigan(3), Montana(9), and Alaska(6)

Table VII. Cont'd.

	Demacutor *venustus* - identified on Ontario hares(1)
Fleas	*Aedes* sp. - female mosquito indentified on Ontario hares(1)
	Simulium *venustrum* - found on one Ontario hare(1)
	Cuterebru sp. (hot fly larva) - identified on one Ontario cottontail(1)
	Fleas uncommon on Michigan hares(3) (7.5%), abundant in Alaska(6)

(1)MacLulich (1937)

(2)Erickson (1944)

(3)Bookhout (1965a)

(4)Doods and Mackiewicz (1961)

(5)Phillip (1938)

(6)Trapp (1962)

(7)Boughton (1932)

(8)Gable and Dougherty (1944)

(9)Adams (1959)

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