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Mechanics of replenishment of a heavily hunted population of snowshoe hares

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FINAL REPORT

State: New York
Project No.: W-105-R

Project Title: Wildlife ecology, behavior and habitat improvement in the Adirondacks.

Study: IX - Mechanics of replenishment of a heavily hunted population of snowshoe hares.

Study Objective: To evaluate the relative roles of natality and immigration in the replenishment of a heavily hunted population of snowshoe hares.

Jobs in this Study: The following jobs are covered in this report:

IX-1. Capturing, marking, track censusing (winter) and position telemetering (summer) of snowshoe hares.

IX-2. Collection of female snowshoe hares for determination of reproductive potential.

IX-3. Analysis and interpretation of data of movements and reproduction of snowshoe hares contributing to changes in population density.

Period Covered:

Jobs IX-1 and IX-2: April 1, 1969 to September 1, 1975.

Job IX-3: April 1, 1969 to March 31, 1976.

(See Narrative Summary, W-105-R-15, dated March, 1975)

Abstract

Hunters in New York State have expressed concern about over-harvesting local snowshoe hare populations. This was an experimental study to determine the mechanisms of replenishment of a heavily hunted (hunting simulated by removal) snowshoe hare population in the central Adirondacks. Mean conception dates for central Adirondack hares are April 10, May 15 and June 14. Mean parturition dates for first, second and third litters are May 17, June 21 and July 21 respectively. Litter sizes for first, second and third litters are 2.07, 3.0 and 2.60 respectively. On the basis of mean litter size and conception rates, the mean number of young produced per female per year is 6.53. This is among the lowest values recorded anywhere. The mean annual survival rate for adult hares determined from mark-recapture data is 0.46. Mean movement distances within trapping periods are 140.6 m for males males and 171.8 m for females. Open areas, logged areas or breaks in cover act as barriers to hare movement. In 254 recorded movements (mark-recapture) only two crossed a two-lane highway and an open marsh. On the experimental portion of the study area, a hare population averaging 20.2 hares (March level, six year mean) was decimated in two alternate years (86 percent removal of the population). Complete replenishment occurred in both instances within one year of decimation. An index based on track count densities weighted by cover type area was found to provide accurate population estimates. About 66 percent of the hare population is trappable by box traps. This bias appeared to be consistent and was found useful in providing absolute estimates of the population. The hare density computed for the experimental portion of the study area was 31 hares/km^2 (83 hares/mi^2). The population density for optimum, dense conifer cover (Base Cover) is 165 hares/km^2 (435 hares/mi^2). This is among the highest densities recorded and suggests that Adirondack hare densities are a function of available cover. Predation (red fox, gray fox, coyote, bobcat and fisher) as determined by snow track surveys declined precipitously in both winters following decimation of the hare population. Thus, after one year following hare decimation, most mammalian predators had not returned, even though hares were present at former levels. Immigration following decimation (in March) appeared to occur throughout the following fall and early winter. Apparently, migratory movement distances of hares exceed normal movement distances. The role of reproduction in replenishing hare populations was modeled. Assuming no immigration or emigration, a population increases itself in one year by a factor of 1.6. This increase is described by the equation Log $P_t = 0.197t +$ Log P_o, where P_t is the March population at time t and P_o is the starting pre-breeding population. This reproductive potential represents a doubling of the population every 1.5 years. Data from the studied population suggest that Adirondack populations are generally stable. A model of a stable hare population shows that one-half of the annual juvenile production is available for emigration. This "exportable fraction" represents about 80 percent of the pre-breeding population.

Most of this fraction may have dissipated by the time hare hunting is at its best in February and March. Thus, the late winter hare population is particularly vulnerable to hunting. This fact may be locally a problem where hare populations are isolated or semi-isolated. The apparent vigor of hare migration may have potential as a management tool. A "biological sink" can be created by purposeful overharvesting of local populations in areas of optimum continuous cover. These depleted areas may attract and hold fall immigrants for late-winter hunting. Adjacent tracts of relatively unhuntable cover would serve as de facto refuges, producing the potential immigrants. Conversely, where certain heavily hunted areas are equivalent to biological sinks (e.g. southern New York) the value of unhunted refuges in replenishing such areas should be investigated. Two important conditions for the effectiveness of the sink concept is that cover between the sink and functional refuge must be continuous and that refuge hare habitat is optimum. Recommendations are as follows: (1) There is no biological reason why the hare hunting season in northern New York could not be extended to the end of March in order to encompass optimum hare hunting conditions in late March. (2) The potential problem of overharvesting isolated or semi-isolated hare populations should be examined. (3) The key factor of cover continuity should be incorporated into State guidelines for conifer plantation management. (4) The "biological sink" idea as well as associated hare habitat management procedures have good potential for private landowners who wish to practice intensive management. Eventually, such intensive management procedures might be promoted through an extension program and establishment of demonstration areas.

Background

The biology and population dynamics of the snowshoe hare *Lepus americanus* have been intensively studied. Many of these research efforts have sought to explain the hare's spectacular cyclic fluctuations and mechanisms of population regulation (e.g. Elton 1935, MacLulich 1937, Green and Evans 1940, Chitty 1950, Meslow and Keith 1968, Dolbeer and Clark 1975, and Windberg and Keith 1976). These studies have been concentrated in the northern and western sections of the hare's range in North America, where its cyclic fluctuations are most pronounced. In the northeastern United States, where the snowshoe hare is prized as a game animal, it has been less studied. In this region, the snowshoe hare is on the southern fringes of its natural range. Not surprisingly, there are some important differences in hare biology in this region compared to more northerly or westerly ranges. For example, litter sizes decrease with decreasing latitude (Keith 1963), with correspondingly lower productivities for the region. Hare populations are possibly more vulnerable than elsewhere, judging from the many local populations which have been extirpated. Intensive trap-and-transfer efforts have been required to reestablish some of these populations (e.g. New York, Dell 1976). In New York, populations are often small and tend to fluctuate less if at all compared to northern and western populations. In sum, one can infer that biological factors affecting snowshoe hare management in the northeastern United States are different enough to warrant careful study. In a general sense, this research effort has addressed the latter need.

More specifically, the study sought answers to snowshoe hare management questions for northern New York. Adirondack hunters have frequently expressed apprehension at "burning out" local hare populations. Are such fears justified? If so, to what extent and under what conditions? The study partly answers these questions and also provides biological information for application in hare management. I thank C.W. Severinghaus and J. Dell of the New York State Department of Environmental Conservation and D.F. Behrend, State University of New York, College of Environmental Science and Forestry, for their contributions in developing the study proposal. Technical coordination was provided by R.W. Sage. The following assisted in hare trapping and telemetry efforts: R.D. Masters, A.T. Stirling, J.E. Wiley, M.J. Tracy, J. Chapman and A. Blanchette.

Study Area and Methods

The study area is a typical, logged, second growth forest tract in the central Adirondacks. It is 1.1 km^2 (0.43m^2) in size, vegetated by a mixture of conifers and hardwoods. Principle species are balsam fir *Abies balsamea*, red spruce *Picea rubens*, eastern white pine *Pinus strobus*, trembling aspen *Populus tremuloides*, large-tooth aspen *Populus grandidentata*, red maple *Acer rubrum*, sugar maple Acer saccharum, yellow birch Betula alleghaniensis and speckled alder Alnus rugosa. Shrubs include black raspberry Rubus occidentalis, blueberry Vaccinium sp. and wild raisin Viburnum cassanoides.

A paved two-lane highway and a stream bisect the study area into north and south sections (Fig. 2). Experimental exploitation of the snowshoe hare population was conducted on the south section, designated the Experimental Area. The north section, the Control Area, was used to monitor the normal, unmanipulated population level. The study area was heavily logged in 1972 and 1973 by the private owners. As a result, the Control Area ceased to serve as a population control in 1973. While the experimental area was also logged, none of the critical Base and Travel Cover classifications (see below) were affected and observations on the logged area were incorporated into the study design so that the effects of logging on the hare population could be determined.

In order to stratify snow track censuses which were used as a basis for population estimates, cover types were classified into four categories according to their significance in hare ecology (see Brocke 1975), namely (1) Base Cover, consisting of dense conifer stands 2.5 to 4.5m in height where hares would spend the day, (2) Travel Cover, including conifer stands 4.5 to 14.0m in height or alder thickets, used by hares as avenues of travel, (3) other cover consisting of second growth hardwood or hardwood-softwood mixtures where hares feed, and (4) clearings and open marshy areas generally avoided by hares. Track counts were stratified into four groups, namely (1) cover class 1 (above), (2) a mixture of cover class 1, 2 and 3, (3) cover class 2 only, and (4) cover class 4. Cover types were mapped using aerial photographs and precise areas of cover sub-groups were determined by planimeter.

Snow track censuses of hares and predators (red fox, gray fox, coyote, bobcat and fisher) were conducted along access trails (see Fig. 2) crossing the study area during the six winters from 1970 through 1975. These access trails were marked with metal tags placed at 25m intervals which served as permanent reference points for all track counts, hare captures and cover classifications. Trails in the snow (tracks) were counted as they crossed the access trail, each trail crossing being given a count of one. Counts were made only on the day following a fresh snowfall ending in the evening of the previous day. In this way, only one night of hare activity was represented in each count. Total track counts were expressed as track densities, i.e., tracks/100m of trail. These track densities were grouped by cover class. Mean track density values (tracks/100m) were computed for (1) Base Cover, (2) Base-Travel Cover mixture and (3) Travel Cover. These mean values (for each winter) were weighted by the total areas within the cover classes to obtain indices of population density.

Hares were trapped, marked and released on both Control and Experimental Areas to determine movement distances, movement patterns and minimum rates of survival. Hare trapping was conducted for periods of approximately 20 days in the fall (October) and in late winter (March). In two alternate years (1971 and 1973) almost all hares were removed from the Experimental Area (as indicated by the absence of tracks) to assess the population response to decimation. These near-total removals also served as accurate counts of the hare population. Hares were captured in metal box traps of the standard Tomahawk design and with live snares (Brocke 1972). Captured hares were sexed and aged by examining genitals and were marked with metal ear tags. All movements were plotted as linear distances between access trail locations on a detailed map. Our original intention was to use mark-recapture data to estimate populations. However, it soon became apparent from hare tracks in the snow that a significant number of hares were deliberately avoiding traps. The untrappable fraction of the population (see Results and Discussion) was subsequently determined to be one third of the population. In response to this bias, standard mark-recapture techniques (e.g. Schnabel and Schumacher-Eschmeyer method, see Wildlife Management Techniques manual, R.H. Giles ed. 1969) were not employed to estimate populations. Rather, the track index method described above was used. This technique was found to be accurate. Additionally, we observed that trapping bias was consistent from year to year so that the bias itself could be used to estimate populations. This was done where snow track indices were not available (for 1970 on the Experimental Area and all years on the Control Area).

Hares were position telemetered using an AVM Model 12 receiver on a frequency of 151 mHz and a hand-held, three element Yagi antenna. The transmitter attached to the neck collar weighed approximately 35g with a range of up to one mile. The life of these transmitters in the field ranged from two to three months. Each transmittered hare was located telemetrically and often visually each day. The bulk of telemetry data were used to determine hare behavior in relation to cover. These results will be reported in detail in a subsequent report (Final Report for W-105-R, Study X. Habitat management for optimum population densities and maximum utilization of snowshoe hares).

Data on reproduction were obtained from female road-killed hares collected during spring and summer months. These hares were collected within a 80 km radius of the study area. Uteri were removed and examined for the presence of embryos or fetuses. The number of young in each litter was recorded. Embryos and fetuses were aged by comparing their weights and lengths to Bookhout's (1965a:79) curves for prenatal age. The conception date for each litter was determined by back-dating the litter age. Parturition dates were calculated on the basis of a 37 day gestation period.

(Severaid 1945). Pregnancy rates were determined using the following assumptions: (1) The pregnancy rate for a given litter period is the fraction of total females collected assumed to have conceived during that period. (2) Pregnant females and females lactating, but not pregnant during the first litter period were assumed to have borne a litter during the period. (3) All females collected during the second litter period were assumed to have produced a litter. A pregnancy rate of 100 percent for the second litter period has been reported by Meslow and Keith (1968) and Dolbeer and Clark (1975). (4) All pregnant females and all lactating females collected 37 days after the first recorded conception date (June 9) for third litters (namely after July 16) were assumed to have produced third litters. In calculating reproductive rates, no allowances were made for prenatal mortality of visible embryos and fetuses. This source of error is probably small. Post-implantation losses reported by Dolbeer and Clark (1975) are 0 to 3.8 percent. Newson (1964) reports values ranging from 5 to 7 percent.

Adult survival rates are based on the number of marked hares captured in a given trapping period stated as a fraction of the hares trapped and marked during a previous period. As some marked hares may have emigrated, these survival rates are minimal. We found an apparent positive trapping bias in hares as 70 percent of all hares captured once were retrapped. One may infer that trapshyness would deter few hares from recapture in subsequent trapping periods.

Several details of research strategy deserve comment. First, the studied hare population was small (about 20 animals), which is typical for the Adirondacks. Hence, the population itself could not be sampled (females killed) in order to obtain data on reproduction because the loss of the samples to the population would greatly affect its dynamics. Hence, data on reproduction were collected from road-killed hares. In any case, there is little reason to believe that reproductive characteristics of road-killed hares were different from those of hares in the study area. Recent findings (Windberg and Keith, 1976) show that reproductive rates of snowshoe hares are unaffected by changes in population density. Second, population census techniques had to be accurate because each unit of a small population is a relatively large percentage of the total. We believe that the census techniques developed in this study, used in conjunction with near-complete removal by box traps and live snares (Brocke 1972) were accurate. Third, there was the question of assessing the relative roles of reproduction and immigration in replenishing the decimated population. While the role of reproduction could be modeled from natality and survival data, the role of immigration had to be experimentally determined. Even if immigration rates were available in the literature (which they are not), the unique characteristics of the study area (ecological barriers to hare movement, etc.) would preclude gross application of such rates. Near-complete decimation of hares was selected as the best experimental choice because the population response to any lesser measure would have included an undeterminable level of both immigration and reproduction. Finally, the experiment was repeated to verify the population response to the treatment applied the first time.

Results and Discussion

Reproduction and Survival

Reproductive data are given in Table 1 and Figure 1. It appears that there are three well defined litter periods in the central Adirondacks, judging from the discrete conception periods. Mean parturition dates for first, second and third litters are May 17, June 21 and July 21 respectively. The earliest and latest calculated parturition dates are May 2 and July 27 respectively. Lactation in road-killed females was observed as late as August 24.

It is noteworthy (Fig. 1) that even though the data represent eight years of collection, data for all years fit the same pattern, i.e., three litters per year. This is not invariably the case for a given geographic region. For example, Dolbeer and Clark (1975) report three litters in one year and two litters in two other years in Colorado. These litter periods were staggered in different years, possibly reflecting climatic differences between years. The spacing of mean conception dates, i.e., slightly more than one month apart is expected with a 37 day gestation period and near-immediate impregnation after parturition. This spacing is typical for snowshoe hares everywhere, regardless of the number of litters.

The litter size ranges from 2.07 for the first litter to 3.0 for the second litter (Table 1). The mean litter size of 2.56 for the Adirondacks is similar to the corresponding mean value of 2.68 reported for Michigan (Bookhout 1965b). The average number of young produced per female surviving the breeding season per year is 6.53 for the Adirondacks and 6.54 for Michigan (Bookhout 1965b). These values are among the lowest reported anywhere. Equivalent values are 6.8 for Minnesota (Green and Evans 1940), 8.6 for Maine (Severaid 1942), 8.2 for Colorado and 11.5 for Utah (Dolbeer and Clark 1975) and 11.3 for Newfoundland (Dodds 1965). Equivalent values for Alberta range from 7.8 to 18.6, depending on the time of the cycle (Meslow and Keith 1968). It is apparent that this relatively low reproductive rate for Adirondack snowshoe hares is an important factor in explaining their regional demographic characteristics.

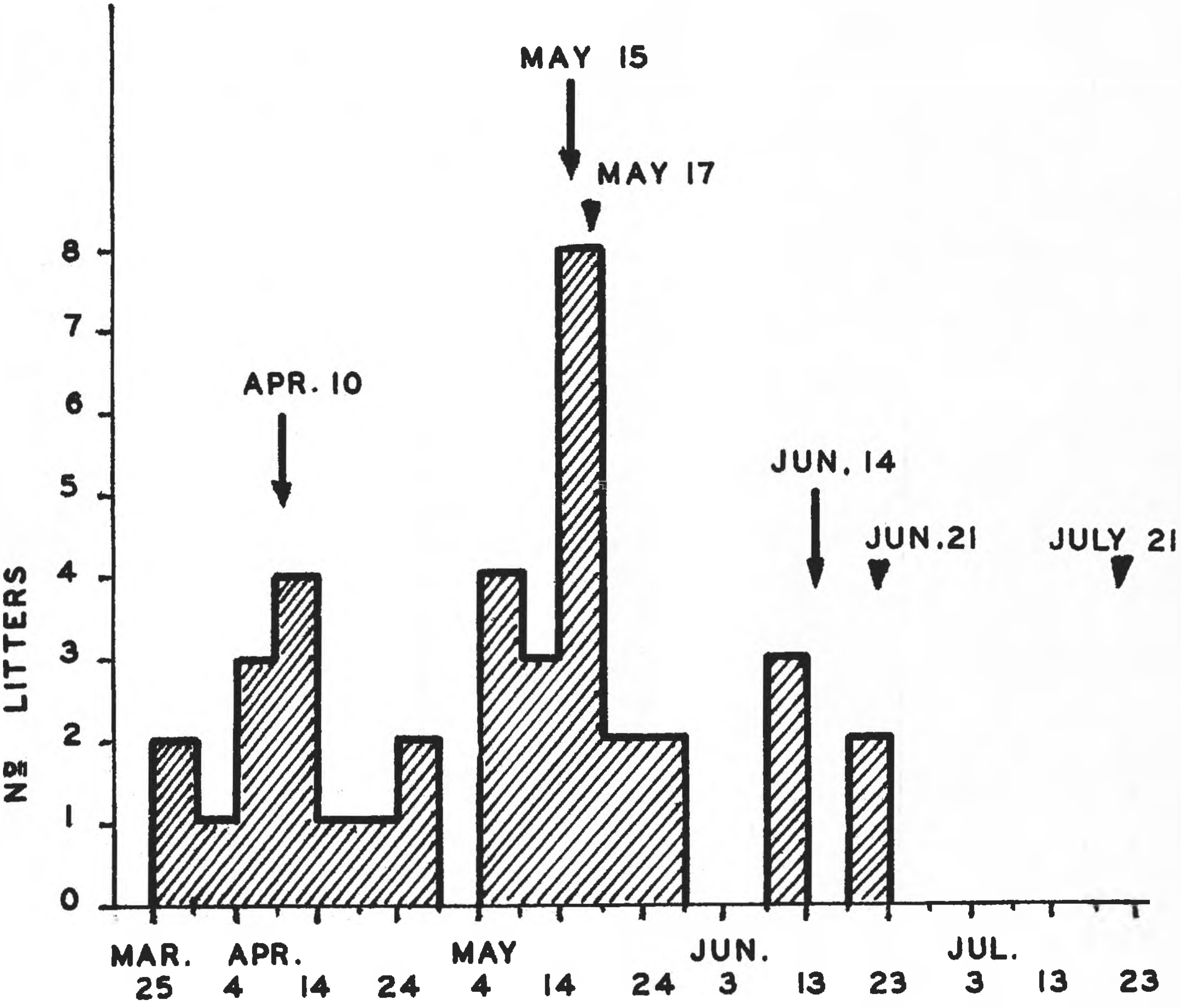
The sex ratio of snowshoe hares trapped on the study area (Experimental and Control Areas) is not significantly different from 1:1. A total of 118 hares were trapped, of which 54 percent

Table 1. Reproductive data for Adirondack snowshoe hares. Sample sizes are in parentheses. For assumptions, see text.

Parameter	Litter 1	Litter 2	Litter 3
Mean Conception Date	Apr. 10	May 15	Jun. 14
Range of Conception Dates	Mar. 26-Apr. 28	May 6-26	Jun. 9-20
Mean Parturition Date	May 17	Jun. 21	Jul. 21
Range of Parturition Dates	May 2-Jun. 4	Jun. 12-Jul. 2	Jul. 16-27
Litter Size ($\bar{x}$ ± S)	2.07 ± 0.83 (14)	3.00 ± 1.20 (19)	2.60 ± 0.89 (5)
Pregnancy Rate	0.94 (17)	1.00[1]	0.61 (18)
Young born per female (Litter size x preg. rate)	1.94	3.00	1.59
Total young per female		6.53	

[1] Assumed rate, see text. The observed rate is 0.96 (25).

Figure 1. Conception periods for snowshoe hares in the central Adirondacks. Data have been grouped into five-day classes. Mean conception and parturition dates for first, second and third litters are shown by arrows and wedges respectively. Data are for the years 1969 through 1976.



MAY 15
MAY 17
APR. 10
JUN. 14
JUN. 21
JULY 21
Nº LITTERS
0
1
2
3
4
5
6
7
8
MAR. 25
APR. 4
14
24
MAY 4
14
24
JUN. 3
13
23
JUL. 3
13
23

Table 2. Survival rates for snowshoe hares in the Experimental Area. Sample sizes are in parentheses.

Age Class	Period	Survival Rates For Period	Survival Rates Annual
Juveniles and Adults[1]	October to March[2] (5 months)	0.62	0.32 (29)
	October to October[3] (1 year)	0.80	0.80 (5)
Adults	March to October[4] (7 months)	0.47	0.27 (19)
	March to March[5] (1 year)	0.45	0.45 (11)
Mean			0.46 (64)

[1] See text.

[2] Data for 1969-70, 1970-71, 1971-72.

[3] Data for 1969-70.

[4] Data for 1970 and 1972.

[5] Data for 1970-71.

were males. This deviation can be expected due to chance (Chi^2 = 0.68, p = 0.3 - 0.5). A 1:1 sex ratio for snowshoe hares has been reported by Newson and DeVos (1964) for Manitoulin Island, Meslow and Keith (1968) for Alberta, and Dolbeer and Clark (1975) for the Rocky Mountains. A significant difference from an even sex ratio favoring males is reported by Dodds (1965), although the difference is less than 5 percent in most samples.

Survival rates for the Experimental Area are given in Table 2. As the continuity of hare survival was disrupted by decimation on the Experimental Area in 1971 and 1973, the sample sizes for individual periods are small. The words "juvenile" and "adult" require explanation. The word "juvenile" refers to an animal *discernable* from genital examination as young of the previous breeding season. These animals are adult sized by October and may be considered as adults by year's end. Furthermore, the ability to distinguish this cohort by genital examination is subject to considerable error in late winter. For all practical purposes, data for the four groupings given here can simply be considered as representative of adult survival. It appears that the age ratio ("adult" and "juvenile" cohorts) of the population is relatively fixed by October (Adams 1959, Meslow and Keith 1968). The latter authors state, "Thus by early fall, young snowshoes apparently have the same mortality rate as older hares."

The mean annual survival rate of 0.46 (equivalent to a monthly rate of 0.938) is higher than those reported by Meslow and Keith (1968) ranging from 0.13 to 0.28, Green and Evans (1940) ranging from 0.28 to 0.36, or 0.22 reported by Adams (1959). The value is almost identical to that of Dolbeer and Clark (1975) namely 0.45. Unlike previous studies and this one which determined survival rates from trapping data, Brand et al. (1975) studied hare survival by following the fate of telemetered individuals. The mean annual rate calculated from their mean values (0.58 and 0.33) is 0.45.

Movements

Linear distances (n=254) between locations where individual hares were trapped are given in Table 3. Differences between means for males and females within each group were tested for significance (t test). None of these means were significantly different (p=.05). One distinctive feature of these distances is that mean values within trapping periods (first category, Table 3) are not much smaller than mean movement distances over semi-annual or annual periods (i.e., fall to spring, spring to spring, spring to fall or fall to fall trapping periods). This is consistent with plotted movements of individual hares which suggest that once the home range of a juvenile hare is established by late fall, it tends to be permanent. Telemetry data (Table 4) reflect the size of spring and summer home ranges (adults) whose greatest diagonal distance is not much greater than individual movements recorded by trapping (Table 3). The shape of a hare's home range and to a lesser extent its daily movements are strongly influenced by the shape of cover patches which it occupies (details of these relationships will be presented in the final report for W-105-R, Study X).

The mean movement distance for males and females (Table 3, mean of all categories) is 170m and 84 percent of all movements were under 210m. Comparable movements for other studies are: 76 percent of all movements under 231m for Alaskan hares (O'Farrell 1965), 78 percent of all movements under 240m for snowshoe hares in Alberta (Meslow and Keith 1968), 98 percent of all movements under 350m for Colorado hares (Dolbeer and Clark 1975). The mean movement distance of males within a single trapping period in this study, namely 140.6m (Table 3) is very similar to the corresponding value of 146m for Michigan males (daily movements, Bookhout 1965 b). However, Bookhout's (1965b)equivalent value of 117m for females is considerably less than the 171.8m (Table 3) recorded here.

A key finding of this study is that open areas or breaks in cover serve as barriers to hare movement. Approximately one-half of the pole timber class of softwood was logged in the Experimental Area during the summer of 1972, leaving small discontinuous patches of forest interspersed with openings. This logged tract coincided almost exactly with the extent and distribution of Travel Cover on the Experimental Area. In the winters following the logging operation, track counts on the logged tract declined to 40 percent of those during the pre-logging period (Table 5). Larger clearings served as a complete barrier to hare movement and any activity recorded for the logged area was confined to the fringes of it. Thus, the data in Table 5 suggest a higher degree of hare activity on the logged tract than was actually the case. Likewise, a permanent clearing in the center of the Experimental Area (Fig. 2), about 70m in width and 140m long, showed a complete absence of hare tracks during 6 winters of observation. Only on a narrow neck of the

Table 4. Spring and summer movements of four snowshoe hares as determined by telemetry.

Individual No. and Sex	Telemetry Period	Telemetered Locations	Greatest distance spanning all locations (m)
1 Male	Mar. 16-28	9	210
2 Male	Mar. 8 - May 23	16	462
3 Female	Mar. 23 - Jun. 11	16	440
4 Male	Mar. 8 - May 25	20	242[1]
Total	-	61	-
$\bar{x}$ (S)	-	-	338(131)

[1] This animal was road-killed in August within 100m of the densest group of telemetered locations.

Table 5. Density of snowshoe hare tracks on surveyed trails in different cover categories of the Experimental Area for the winters of 1971 to 1974. Track densities are given per 100m of trail for a total of 22 surveys.

	Cover Classification			
Parameter (1971-1974)	Base Cover 425m (n=22)	Base-Travel 2525m (n=22)	Travel Cover[1] 1925m (n=11)	Logged Travel Cover[2] 1925m (n=11)
Tracks/100m $\bar{x} \pm 2S\bar{x}$	4.8 ± 1.6	1.6 ± 0.4	1.5 ± 0.8	0.6 ± 0.3
Index, relative intensity of use. Logged travel cover = 1.00.	8.0	2.7	2.5	1.00

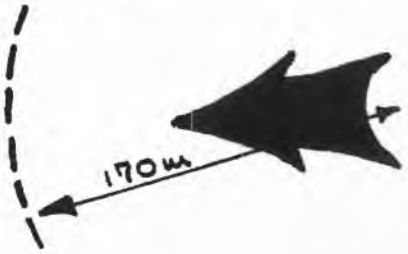
[1] Data for the years 1971 and 1972.

[2] Data for the years 1973 and 1974.

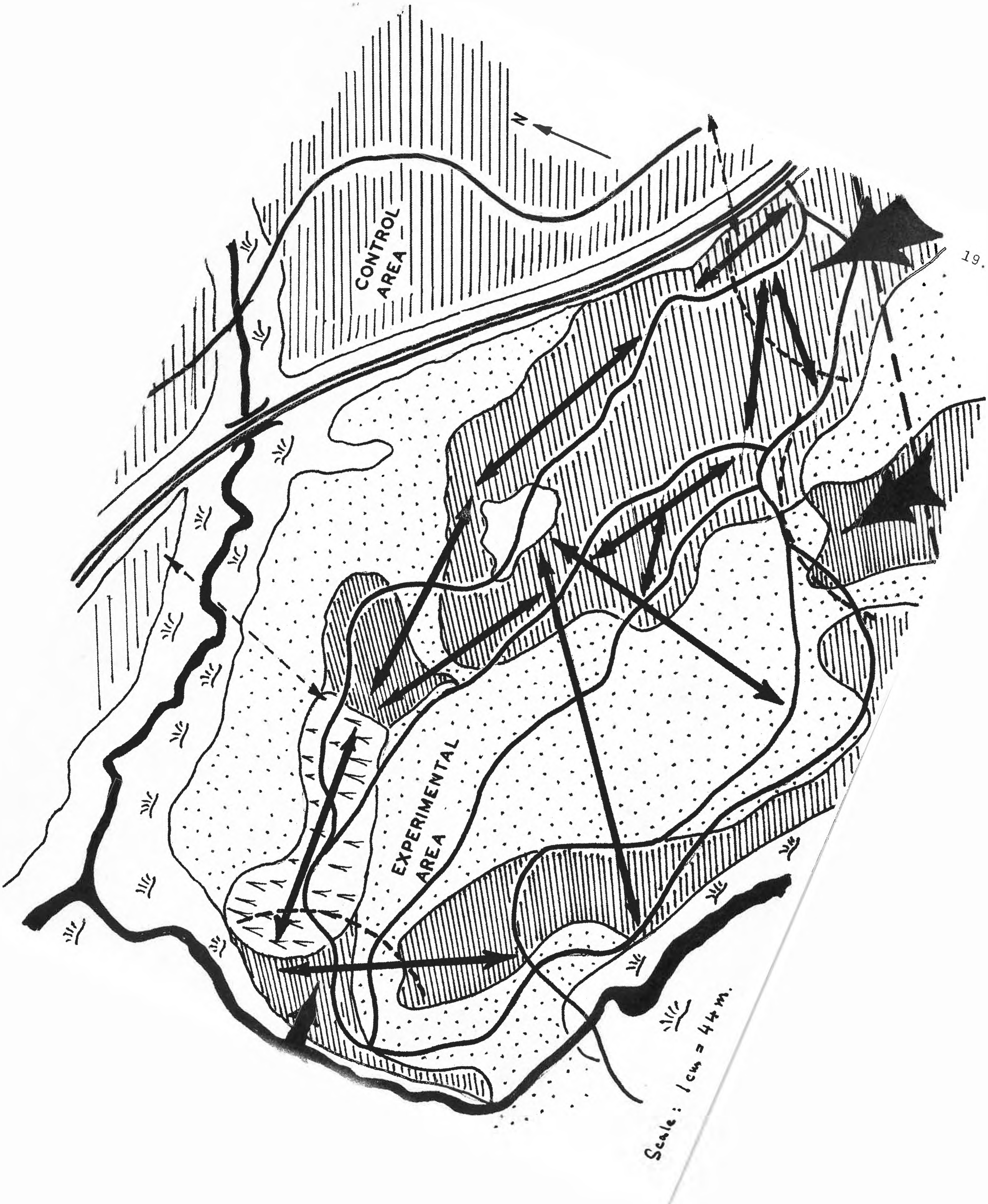
Figure 2. The study area, showing cover type classifications, movement vectors and inferred immigration routes.

LEGEND

⅄	Access Trail
═	Highway
⋀⋀	Base Cover (see text)
▨	Base Cover-Travel Cover mixture
⁘	Travel Cover, Logged Area
ѱ	Open Marsh (Barrier to hare movement)
☐	Open clearings, roadsides (Barriers to movement)
⟷	Vector representing general movement patterns
◄– – – –►	Crossing point of individual hare



Inferred immigration route. Arc equals mean movement distance of 170m.


N
CONTROL AREA
EXPERIMENTAL AREA
Scale: 1 cm = 44 m.

clearing where conifers straggled across it, did hares occasionally cross.

We were surprised to find that the two lane highway and open marsh, together dividing the Experimental Area from the Control Area (Fig. 2) apparently were a major barrier to hare movement. The state highway and its shoulders created a gap in the forest about 35m wide, while the open marsh ranged in width from 70 to 130m. In a total of 254 cases where hares were trapped, marked and released on both sides of this dividing strip, there were only two instances in which hares marked on one side of the strip were subsequently trapped on the other. These two instances are recorded by dotted lines in Figure 2. (Other major vectors of travel are also indicated in Fig. 2.) While some movements across the highway did occur at certain points, judging from the presence of road-killed hares in spring and summer, apparently this strip served as a barrier to many hares. The same appeared to be true for the marsh southwest of the Experimental Area.

Population Response to Decimation

There were two controls for the experimental decimation of hares (conducted in the alternate years of 1971 and 1973) namely (1) no treatment in the years 1970, 1972, 1974 and 1975, with accurate monitoring of the manipulated population on the Experimental Area in those years, and (2) a monitoring of the population level in the adjacent Control Area. The latter control was desirable because if the decimated population had failed to replenish itself, that failure might have been due to a region-wide decline in hares. As indicated previously, the second control was only available for three years. Relative population levels as indicated by trapping success rates are given in Table 6. Indices of the population level on the Control Area for the first three years of the study are 0.7, 1.0 and 1.0 respectively, suggesting that the unmanipulated population adjacent to the Experimental Area was relatively stable. Following 1972, our casual observations suggested that the regional hare population remained stable.

Response of the population to decimation is given in Table 7. The population declined slightly from the initial level to March of 1971, when 13 hares were removed from the area. Two hares remained at opposite ends of the study area, judging from tracks in the snow. Thus, the pre-removal population level was set at 15. One of the animals which remained, a male, had been captured in March of 1970 and was subsequently trapped in October of 1972.

By March of 1972, the population had replenished itself completely to an estimated 15 animals. The population increased slightly to an estimated 22 animals by March of 1973. This estimate was based on the removal of 19 hares, leaving three in widely

Table 6. Box trapping success indices of snowshoe hare population levels on the Control Area for the periods 1969-70, 1970-71 and 1971-72. Data for fall and late winter trapping efforts have been combined for each period.

	Period			
Parameter	1969-70	1970-71	1971-72	Mean ± S
Individual hares captured per period	25	21	25	23.7 ± 2.3
Trap nights per period	2205	1290	1533	1676 ± 474
Trapping success: Individual hares captured per 100 trap nights	1.1	1.6	1.6	1.5 ± 0.3
Population index (1970-71 value equals 1.0)	0.7	1.0	1.0	-

Table 7. Response of the snowshoe hare population to decimation on the Experimental Area. Population estimates are for March of the year.

Treatment or Parameter	Year						Mean ± S All Years
	1970	1971	1972	1973	1974	1975	
Experimental Treatment (March of the year)	None	Decimation 86 percent removal of population	None	Decimation 86 percent removal of population	None	None	-
Population estimate for Experimental Area (64.3 ha, 159 A)	24[1]	15[2]	15[3]	22[4]	21[3]	24[3]	20.2 ± 4.2
Ratio of 1973 population estimate to that of 1971[5]	-	1.0	-	1.5	-	-	-
Population density index based on track surveys[6]	-	1.0	1.0	1.4	1.4	1.6	-
Population index based on box trapping success[7]	1.6	1.0	1.3	1.5	-	-	-

[1] Estimate derived as follows: Pop. index based on trapping success x 1971 estimate based on removal, i.e. 1.6 x 15 = 24.

[2] Thirteen hares were removed, leaving two hares as indicated by tracks in the snow, giving a total estimate of 15.

[3] Estimate derived by multiplying population density index for the year by the 1971 population estimate by removal.

[4] Nineteen hares were removed leaving 3 hares as indicated by tracks in the snow, giving a total estimate of 22 hares.

[5] Values for 1972, 1974 and 1975 are not given; these are identical to population density indices based on track surveys because population estimates were derived from the latter.

[6] Values from Table 8.

[7] Values from Table 9.

Table 8. Density of snowshoe hare tracks on surveyed trails of the Experimental Area for the winters of 1971 through 1975.

	1971 (n = 5)		1972 (n = 6)		1973 (n = 3)		1974 (n = 8)		1975 (n = 11)	
Cover Classification	Tr/100 m $\bar{x} \pm 2 S\bar{x}$	Index[1] Pop. Dens.	Tr/100 m $\bar{x} \pm 2 S\bar{x}$	Index Pop. Dens.	Tr/100 m $\bar{x} \pm 2 S\bar{x}$	Index Pop. Dens.	Tr/100 m $\bar{x} \pm 2 S\bar{x}$	Index Pop. Dens.	Tr/100 m $\bar{x} \pm 2 S\bar{x}$	Index Pop. Dens.
Base Cover (425 m trail)	5.0 ± 1.7	14.5	1.8 ± 1.0	5.2	4.5 ± 5.3	13.0	7.2 ± 3.2	20.9	6.2 ± 1.3	18.0
Base-Travel Cover Mixture (2525 m trail)	1.2 ± 0.5	30.4	1.6 ± 1.1	40.5	2.0 ± 1.7	50.6	1.6 ± 0.5	40.5	2.2 ± 0.6	55.7
Travel Cover Pre-logging (1925 m trail)	1.7 ± 1.1	-	1.4 ± 1.1	-	-	-	-	-	-	-
Travel Cover Post-logging (1925 m trail)	-	-	-	-	0.6 ± 0.3	-	0.6 ± 0.4	-	0.9 ± 0.2	-
TOTALS[2]										
Raw Index of Population Density[1]	-	44.9	-	45.7	-	63.6	-	61.4	-	73.7
Population Density Index (multiple of lowest value)	-	1.00	-	1.02	-	1.42	-	1.37	-	1.64

[1] Population Density Index = Track Density/100 m of trail x Area of Cover Class (ha), for Base Cover and Base-Travel Cover only.

[2] Total Excludes Values for Travel Cover

Table 9. Box trapping success indices for March snowshoe hare population levels on the Experimental Area for the years 1970 through 1973.

	Period				
Parameter	March 1970	March 1971	March 1972	March 1973	Mean ± S
Individual hares captured per period	13	8	11	13	11.2 ± 2.4
Trap nights per period	926	924	966	987	950 ± 30
Trapping success: Individual hares captured per 100 trap nights	1.4	0.9	1.1	1.3	1.2 ± 0.2
Total individual hares captured per period using box traps and live snares	19[1]	13	11[2]	19	-
Box-trapped fraction of total hares captured	0.68	0.61	-	0.68	0.66 ± 0.4
Population index based on trapping success (see above); 0.9 hares/100 trap nights = 1.0	1.6	1.0	1.3	1.5	-

[1] These hares were not removed, unlike population estimates by removal.

[2] Total reflects box trap captures only; no live snares employed in 1972.

Table 10. Mean March snowshoe hare population densities computed for cover types classifications within the Experimental Area.

Area	Hares/total area	Hares/ha(A)	Hares/km^2(mi^2)
Total Area (64.3 ha, 159 A)	20.2	0.31 (0.13)	31 (83)
Base Cover (2.9 ha, 7.1 A)	4.8	1.65 (0.68)	165 (435)
Base-Travel Cover (25.3 ha, 62.6 A)	15.4	0.61 (0.25)	61 (160)

separated sections of the study area. Again, the population replenished itself by March of 1974. For all years, the March population did not deviate much from the mean value of 20.2, despite drastic treatment in two years.

Assessment of population response in this study depended heavily on the accuracy of population estimates. The primary basis for these estimates was provided by track surveys weighted by the area of cover type (see Table 8). Unexpectedly, indices based on trapping bias (Table 9) also appeared to be accurate, and hence were also used. Comparison of independently derived values for 1971 and 1973 (Table 7) provide a basis to assess the accuracy of these indices. The March population in 1971 and 1973 was essentially known. The relationship of these populations to each other is 1 to 1.5 (Table 7). The density indices based on track surveys for the same years are 1.0 and 1.4 respectively, while the population indices based on box trapping success are 1.0 and 1.5 respectively. The close correspondence of these independent ratios to each other suggests that the population estimates derived from them in other years are relatively accurate. A farther indication that box trapping success can be usefully applied as a relative indicator of the population level is the consistent trapping bias shown in Table 9. The box-trappable fraction for three years did not deviate greatly from 66 percent

Using the mean population estimate (20.2, all years) for the Experimental Area, the mean density of hares was calculated for Base Cover and Base Cover-Travel Cover mixture using mean track densities (all years) for these two cover classifications (Table 10). The March population density for the total area was 31 hares/km^2 (83 hares/mi^2). However, for Base Cover alone, the density was 165 hares/km^2 (435 hares/mi^2). These densities compare to the following pre-breeding densities reported from other locations: 25 hares/mi^2 in Michigan (Bookhout 1965 a) 75 hares/km^2 in Colorado (Dolbeer and Clark 1975) and 23 to 622 hares/mi^2, depending on the cycle, in Alberta (Meslow and Keith 1968). It appears that the density of 31 hares/km^2 (83 hares/mi^2) for the Experimental Area is similar to densities reported elsewhere. However, where cover is optimum (Base Cover), Adirondack hare populations may reach densities close to the highest recorded anywhere.

Predation

Tracks of predators including the red fox, gray fox, coyote, bobcat and fisher were routinely surveyed during the winters of 1971 through 1974. These track counts were converted to densities (tracks/100m of trail) and each track density within a given cover classification weighted by the area of that cover type to give an Activity Index (Table 11). The relative levels of winter activity

Table 11. Density of predator tracks on surveyed trails of the Experimental Area for the winters of 1971 to 1974.[1]

	1971 (n = 5)		1972 (n = 6)		1973 (n = 3)		1974 (n = 8)		1971-74	
	Tracks/ 100m	Activity Index	Tracks/ 100m	Activity Index	Tracks/ 100m	Activity Index	Tracks/ 100m	Activity Index	Mean Tracks/ 100m	Mean Activity Index
Base Cover	0.19	0.55	0.04	0.12	0.16	0.46	0.00	0.00	0.10	0.28
Base-Travel Cover Mixture	0.09	2.28	0.01	0.25	0.22	5.57	0.04	1.01	0.09	2.28
Travel Cover Pre-Logging	0.08	2.38	0.00	0.00	-	-	-	-	0.04	1.19
Travel Cover Post-Logging	-	-	-	-	0.15	4.47	0.06	1.79	0.10	3.13
Total, Raw Index of Activity	-	5.21	-	0.37	-	10.50	-	2.80	-	4.72
Activity Index Multiple of lowest value	-	14.1	-	1.0	-	28.4	-	7.6	-	
Experimental Treatment	86% Removal of Hare Population		None		86% Removal of Hare Population		None		-	

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[1] Track surveys for red fox, gray fox, coyote, bobcat and fisher. These track surveys were made prior to removal of snowshoe hares in 1971 and 1973.

for the four years were remarkable and unexpected. In the winter of 1972, following the decimation of hares in March of the previous year, a 14 fold decline in activity was observed. Predatory activity of all species was essentially absent. Again in 1974, there was a drastic decline in predator activity to almost one-fourth of the pre-decimation level of March 1973. We hypothesize that the near-complete removal of hares in March of 1971 and 1973 left little stimulus for predators in the study area during spring of those years when the reproductive season made their needs most critical. However, it is noteworthy that this possibly learned response carried into the winter of the following year by which time the hares were again present on the Experimental Area.

Mechanics of Replenishment

By design, replenishment of the Experimental Area had to be largely by immigration. It is clear that within one year of decimation, replenishment had occurred following both decimations (Table 7). It appeared from our trapping records that few (if any) hares immigrated from the north (Control Area) across the highway and open marsh into the Experimental Area. Likewise, the open marsh to the southeast appeared to be a major ecological barrier (Fig. 2). The principle directions of replenishment were probably along the southeast and west borders of the study area where suitable cover provided continuous avenues of travel. Together, these borders (1170m) comprise about 34 percent of the total Experimental Area periphery (3400m).

As hares were not trapped to the southeast and west of the Experimental Area, exact locations of ingress are not available. Four hares were captured on the Experimental Area in October, 1971, seven months after decimation. Three of these animals were subsequently captured in March, 1972. Recapture locations for these three animals showed ranges in the west, northwest and central sections of the Experimental Area which were occupied by these animals both in October and March. Eight hares not trapped in October, 1971 were captured in March, 1972. Seven of these individuals showed movement patterns restricted to the eastern and southeastern one-half of the study area. The remaining individual set up a range in the western Base Cover area.

The March, 1972 population estimate for the Experimental Area is 15 (Table 7). The number of hares actually captured in October 1971 was 4. If this number represents 66 percent of the population actually present in October (on the basis of trapping bias, Table 9), then the inferred October population was 6. On this basis, the hare population had apparently increased by nine individuals from October to March, suggesting that immigration continued throughout the fall and winter months.

The bulk of immigration in the 1971-72 fall and winter periods appeared to be from the southeast, judging from captures and recaptures of individual hares, as noted above. A farther indication that this was true is provided by a comparison of track densities for different years in Base Cover (Table 8). The Base Cover mean track density of 1.8 tracks/100m of trail for March of 1972 is considerably lower than those for all other years. The mean values for 1972 (1.8) and 1971 (5.0) are significantly different ($p=.05$, $t=3.2$). Thus, it appears that this patch of optimum cover in the western part of the Experimental Area was not wholly occupied by March of 1972.

A reconstruction of the immigration sequence for 1973-74 is not possible because trapping was not conducted in the fall of 1973. However, by February, tracks in the snow showed that immigrants had penetrated all sections of the area. The mean Base Cover track density for 1974 (7.2 tracks/100m of trail, Table 8) was the highest recorded for any year. Perhaps a greater percentage of hares moved in from the west.

General movement characteristics of hares (Table 3) are not very helpful in reconstructing the immigration picture. The mean movement distance for all hares (170m, from Table 3) is barely enough to carry hares into the study area from its periphery (see arcs, Fig. 2). The mean maximum movement distance of all samples over 10 in Table 3 is 575m. This distance is equivalent to movements from the eastern and western boundaries of the Experimental Area to its center. It appears that normal movement distances of hares are exceeded when they are seeking new range.

The role of reproduction in replenishing Adirondack hare populations was modeled. Assumptions for models are based on data collected in this study and from published information. Two models were computed for an increasing population beginning with 20 and 100 animals respectively. These models simply illustrate the reproductive potential of Adirondack snowshoe hare populations. Two other models were computed for stable Adirondack hare populations, beginning with 20 and 100 animals respectively. Assumptions for these models are:

1. Production of 1.95, 3.00 and 1.59 young by each female alive in May (first litter), June (second litter) and July (third litter) respectively.

2. An annual survival rate for adults of 0.46 (from Table 2), equivalent to a monthly survival rate of 0.938.

3. A monthly survival rate for juveniles of 0.871 from birth through October. This value is based on juvenile survival rates determined by telemetry (Brand et al. 1975). These investigators give survival rates for periods as follows:

Table 12. Model of an annual cycle of a snowshoe hare population beginning with a pre-breeding population of 20 animals, assuming no net immigration or emigration. For other assumptions, see text.

Month	Adult Population	Juveniles Increment	Juveniles Population	Total Population
March	20			20
April	19			19
May (Litter 1)	18	18	18	36
June (Litter 2)	16	24	40	56
July (Litter 3)	15	11	46	61
August	14		40	54
September	14		35	49
October	13		30	43
November	40			40
December	37			37
January	35			35
February	33			33
March	31			31

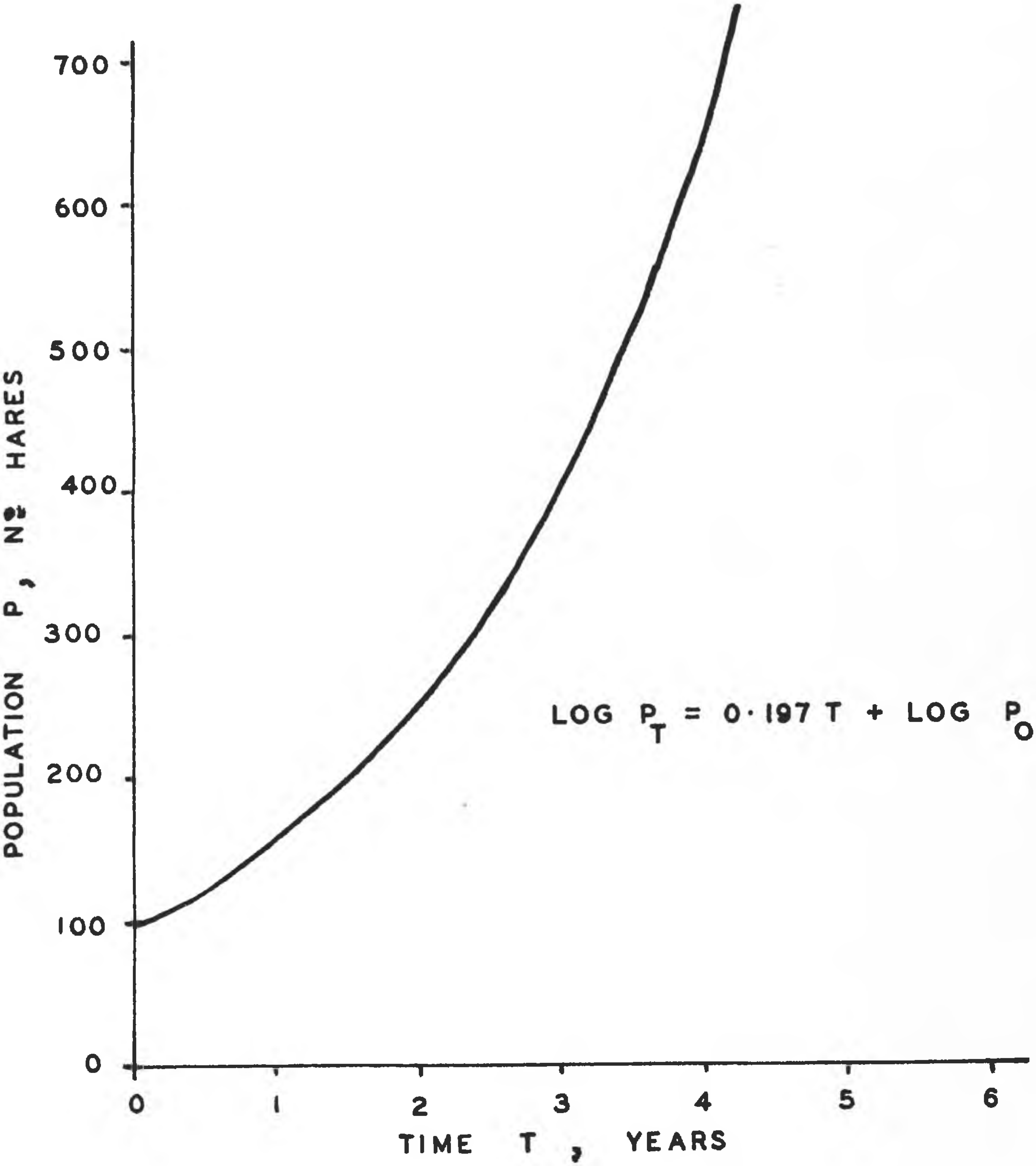
Table 13. Model of an annual cycle of a snowshoe hare population beginning with a pre-breeding population of 100 animals, assuming no net immigration or emigration. For other assumptions, see text.

Month	Adult Population	Juveniles Increment	Juveniles Population	Total Population
March	100			100
April	94			94
May (Litter 1)	88	85	85	173
June (Litter 2)	83	126	200	283
July (Litter 3)	78	62	236	314
August	73		205	278
September	68		178	246
October	64		155	219
November	205			205
December	192			192
January	180			180
February	169			169
March	158			158

Table 14. Factors relating monthly population levels to the March population level (both pre-breeding and post-breeding). Factors were computed from the model for an increasing hare population (Table 13).

Month	Factor March, pre-breeding	Factor March, post-breeding
March	1.0	0.6
April	0.9	0.6
May	1.7	1.1
June	2.8	1.8
July	3.1	2.0
August	2.8	1.7
September	2.5	1.5
October	2.2	1.4
November	2.0	1.3
December	1.9	1.2
January	1.8	1.1
February	1.7	1.1
March	1.6	1.0

Figure 3. Annual increase in the pre-breeding level of a snowshoe hare population, beginning with a pre-breeding population of 100 animals. No net emigration or immigration is assumed.



POPULATION P, Nº HARES
700
600
500
400
300
200
100
0
0
1
2
3
4
5
6
TIME T, YEARS
LOG P_T = 0·197 T + LOG P_O

Table 15. Model of an annual cycle of a stable snowshoe hare population beginning with a pre-breeding population of 20 animals. Net emigration is assumed. For other assumptions, see text.

	Adult		Juveniles			
Month	Population		Increment	Population		Total Population
March	20					20
April	19					19
May (Litter 1)	18		18	18		36
June (Litter 2)	16		24	40		56
July (Litter 3)	15		11	46		61
August	14			40		54
September	14			35		49
October	13	15	← Recruitment	30		43
November	26			↓	Emigration	26
December	25			↓		25
January	23			↓		23
February	22			↓		22
March	20			↓		20

↓

15

Table 16. Model of an annual cycle of a stable snowshoe hare population beginning with a pre-breeding population of 100 animals. Net emigration is assumed. For other assumptions, see text.

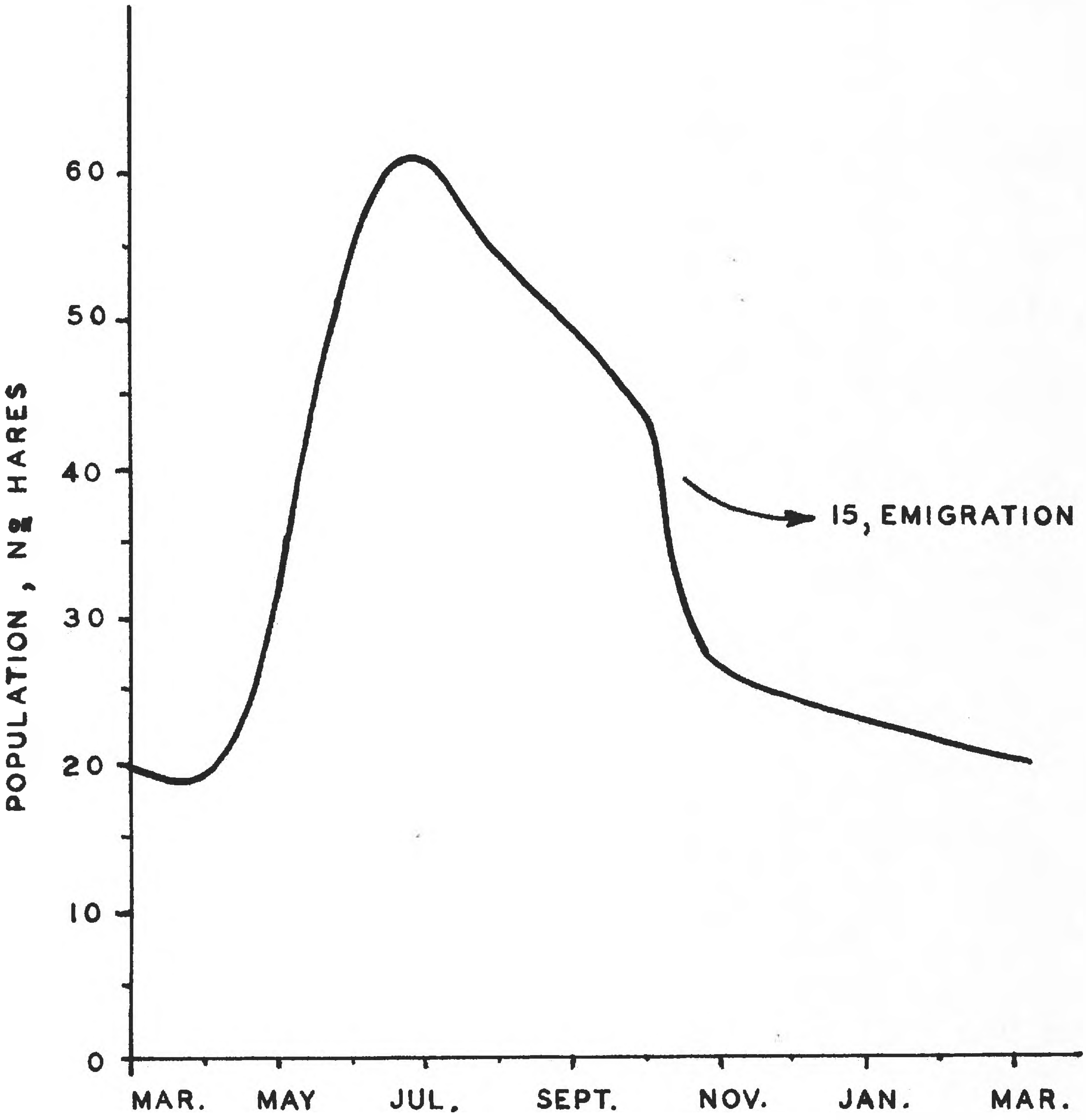
Month	Adult Population		Juveniles Increment	Juveniles Population		Total Population
March	100					100
April	94					94
May (Litter 1)	88		85	85		173
June (Litter 2)	83		126	200		283
July (Litter 3)	78		62	236		314
August	73			205		278
September	68			178		246
October	64	75	← Recruitment	155	↓	219
November	130				Emigration	130
December	122				↓	122
January	114				↓	114
February	107				↓	107
March	100				↓	100

80

Table 17. Factors relating monthly population levels to the March population level. Factors were computed from the model of a stable hare population (Table 16).

Month	Factor
March	1.0
April	0.9
May	1.7
June	2.8
July	3.1
August	2.8
September	2.5
October	2.2
November	1.3
December	1.2
January	1.1
February	1.1
March	1.0

Figure 4. Annual cycle of a stable Adirondack snowshoe hare population, beginning with a pre-breeding population of 20 animals. No net immigration is assumed; emigration of 15 hares occurs in October.


POPULATION , Nº HARES
0
10
20
30
40
50
60
MAR.
MAY
JUL.
SEPT.
NOV.
JAN.
MAR.
15, EMIGRATION

For 15 to 90 days, 0.69 and 0.63 (two years respectively) and for 91 to 180 days, 0.67 and 0.63 (two years respectively). A rate of 0.66 (three months) was selected as representative for the model. This is equivalent to a monthly rate of 0.871.

4. For the two models of an increasing hare population, illustrating reproductive potential, no net emigration or immigration is assumed.

5. For the two models of a stable hare population, net emigration is assumed to occur in late October.

Models assuming no net immigration or emigration are given in Tables 12 and 13 for populations beginning with 20 and 100 animals respectively. Factors relating monthly population levels to March (pre-breeding and post-breeding) are given in Table 14. Assuming that no net immigration or emigration were to occur in the Experimental Area, a population of 20 animals could increase in one year by 11 individuals to a total of 31. Or conversely (using Table 14, second column), 12 animals would have to be alive in March of Year No. 1 to produce 20 animals in Year No. 2. This reproductive potential for successive years is illustrated in Fig. 3. The population increase is described by the equation:

$$\text{Log } P_t = 0.197t + \text{Log } P_o$$

where P_t is the March population at time t and P_o is the starting pre-breeding population. This reproductive potential represents a doubling of the pre-breeding population every 1.5 years.

More realistically, snowshoe hare populations in the Adirondacks are probably stable in most years, although hares are noticeably more common in some years. It appears that the hare population on the Control Area remained relatively stable in three successive years (Table 6). While there was a slight population decline on the Experimental Area from 1970 to 1975 (Table 7), the population remained stable from 1974 to 1975. The rapid replenishment of the Experimental Area suggests that a surplus of hares must emigrate from each population each year, possibly contributing to local population stability. The mortality among these emigrants must be high if most optimum coverts are normally occupied by resident hares. Population stability and emigration are illustrated by models in Tables 15 and 16, beginning with 20 and 100 animals respectively. Assuming the same reproduction and survival rates as in previous models, the model in Table 15 (illustrated in Fig. 4) shows that 15 animals are available for emigration in October from a pre-breeding population of 20 animals. This "exportable fraction" is very nearly the number of the pre-breeding population. The model suggests that to replenish the Experimental Area through immigration, an area slightly larger than the Experimental Area contributed its exportable fraction. These relationships are also illustrated in Table 16 as they would apply to a hypothetical pre-breeding population of 100 animals. Factors relating the monthly population levels to the March level are given in Table 17. The models in Table 15 and 16 illustrate a biological "achilles heel" of snowshoe hare hunting and management, namely that the pre-breeding population can be potentially decimated in late winter when hare hunting is at its best. In a hypothetical example, a given tract of cover has a carrying capacity of 20 hares and due to its isolation, no immigration takes place. If that population were to be hunted in October, 15 hares (the exportable surplus) could be removed and the March population would remain at 20 animals. If, however, the hare population were exploited in late winter after the population had lost its surplus, removal of 15 animals would have a different effect. If 5 hares were removed in January, February and early March respectively for a total of 15 hares and assuming added normal mortality, only 6 hares would remain by March (Table 15). It would take three years (Table 14) for that population to recover fully.

The data in Table 15 and 16 suggest that on the basis of replenishment by reproduction alone, only about one-third of the late winter population can be safely removed. This "achilles heel" would not be a problem in any area where continuous tracts of cover provide ready avenues of replenishment through immigration. However, in areas of southern and western New York where isolated plantations or coverts may exist, especially where highways and cultivation may create barriers to movement, there is apparently a real local danger of overharvest.

The apparent intrinsic strength of hare migration itself appears to have potential as a management tool. For example, in the Adirondacks where continuous avenues of Travel Cover provide ready means of replenishment by immigration, a "biological sink" can be created by purposely overharvesting the population in a readily huntable area. This area, depleted of hares, would draw the net hare production from surrounding less exploitable coverts (de facto refuges) in late fall, holding this normally lost fraction for late winter hunting. Stated differently, the "sink" area of optimum cover would greatly increase the survival of the surplus juveniles until late winter hunting.

Conversely, in southern New York where certain heavily hunted areas are equivalent to biological sinks, the value of unhunted hare refuges should be investigated. For example, a refuge established adjacent to a grouping of overharvested tracts might be tested as a variation of the sink concept. Two important conditions for the effectiveness of the sink concept is that cover between the sink and the refuge must be continuous, and that hare habitat on the refuge is optimum to maximize annual production.

Finally, to what extent reduced predation on the Experimental Area increased the survival of immigrant hares can only be guessed at. Nellis et al. (1972) found that predation by lynxes accounted for 8.0 to 37.1 percent of total snowshoe hare mortality between December and March in Alberta. It is probably safe to say that some improvement in hare survival did occur as a result of decreased predation and that this increased survival rate may have contributed to the rapid population replenishment.

Recommendations

1. Findings of this study indicate that overharvesting of snowshoe hare populations is unlikely where continuous tracts of hare cover provide ready avenues for replenishment by immigration. Therefore, it may be advisable to extend the snowshoe hare hunting season in northern New York, where such continuous habitat conditions commonly exist. In the Adirondacks, hare hunting conditions in many years are not optimum until mid-February. Extension of the season to the end of March would add two weeks of optimum conditions, increasing recreational benefits from hare hunting.

   The mean conception date for first litters in the central Adirondacks is April 10; the earliest recorded conception date is March 26. Hence, extension of the snowshoe hare hunting season to the end of March would not interfere substantially with hare reproduction.

2. Modeling of annual population cycles of Adirondack snowshoe hares suggests that a potential problem of over-exploitation may exist in isolated hare habitats. It may be advisable to examine this problem in greater detail, particularly as it may apply to the Catskill region and western New York. Where such problems exist, there may be an opportunity through local extension programs to alert sportsmen and enlist their efforts in preventing overharvest of local hare coverts.

3. Findings of this study indicate that migrant juveniles will readily replenish overharvested areas where continuous tracts of conifer cover connect major hare habitats. Consequently, the New York State Department of Environmental Conservation might propose simple guidelines for the layout, planting and rotation cutting of conifer plantations on State lands which would insure the production of effective hare coverts in the future. Such simple measures may increase recreational benefits from hare hunting many fold. Additionally, as the snowshow hare is the "staff of life" for so many interesting predators, the presence of such predators due to the presence of hares may be attractive to other segments of the public.

4. The findings of this study suggest that snowshoe hare populations can be intensively managed on a local scale to increase hare production for hunting. The concept of an overharvested area, creating a "biological sink" to hold migrant juveniles for late winter hunting should be developed and tested. Such techniques (and others involving habitat management) might ultimately be promoted among private landholders through an extension program. Demonstration areas on state and private lands might be established for this purpose.

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Principal Wildlife Biologist

Date

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Date