SPACING BEHAVIOR OF SNOWSHOE HARES IN RELATION

TO THEIR POPULATION DYNAMICS

by

STANLEY A. BOUTIN

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Department of ___Zoology___

The University of British Columbia
2075 Wesbrook Place
Vancouver, Canada
V6T 1W5

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ABSTRACT

The importance of spacing behavior on snowshoe hare population dynamics was studied in the Kluane Lake, Yukon area from May 1978 to July 1979. Two study sites, each consisting of a 9.29 ha live-trapping grid, were used to capture and tag animals. Numbers were increasing over the study with May breeding densities going from 8 in 1978 to 20 in 1979. The increase was a result of higher than average (12.25 young caught per female) natality rates. Yearly juvenile and adult survival rates were equal at 20%.

A total of 116 hares were equipped with radio-transmitters during the study. These were monitored to determine home range locations and individual movements. Home ranges overlapped by at least 30% between and within sexes throughout the year. Home ranges averaged larger for males (4-8 ha) than females (3-5 ha). During periods of birth, females contracted the size of their home range but not significantly. 14 radio-tagged individuals dispersed during the study. They moved an average of 1045 m and were from all age and sex classes with the exception of adult males.

To determine the importance of spacing behavior on breeding females' home ranges and movements I removed a small group of individuals from a much larger group of radio-tagged animals. The initial removal was done 10 days before the birth of the first litters and was then repeated 10 days before birth of the second litters. Home ranges were monitored before and after each removal and compared to a control area. Females did not increase their use of the removal area nor was it colonized by

individuals from beyond the ring of radio-tagged animals. This suggests that breeding female densities were not limited by spacing behavior. Females did shift use of their home range after the removal by spending up to 30% more time on the removal side of their range. This suggests that females use their range in a manner that avoids interaction.

Adult females were removed from one of the study areas during the late breeding season to assess their influence on juvenile movements and survival. There were no significant differences in these aspects between the manipulated area and a control. However, telemetry showed that juvenile and adult female home ranges overlapped little on the control area during September. The movements to create this situation were done by juveniles at a time before they could be trapped or radio-tagged. This suggests that some juveniles may leave their parents' home ranges at a time prior to which is detectable by conventional trapping and telemetry. The need for further investigation in this area is stressed.

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1. INTRODUCTION

The snowshoe hare (_Lepus_ _americanus_) is known to exhibit regular 10 year population cycles throughout much of its range (Keith 1963). Although this phenomenon has attracted widespread interest, causal mechanisms are still unknown. Work to date has been primarily concerned with the relation of hare demographic changes to food supply and predation (Keith 1974; Keith and Windberg 1978). Few studies have examined the behavior of snowshoe hares, which is particularly interesting because behavior is rapidly being recognized as an important component of the population dynamics of a number of species (Krebs and Myers 1974; Watson and Moss 1970).

There are two major hypotheses which attempt to explain the snowshoe hare cycle. The first, formulated by Chitty (1960), attempts to explain all small mammal cycles and contends that "... all species are capable of limiting their own population densities without either destroying the food resources to which they are adapted, or depending on enemies or climatic accidents to prevent them from doing so." In contrast, Keith (1974) states that snowshoe hares are "... incapable of self-regulation below densities determined by available food supplies." Chitty feels that aggressive spacing behavior acts to limit numbers below that dictated by food supplies whereas Keith (1974) feels behavior is unimportant and hare numbers are determined directly by a combination of food supply and predation. Examining the effect of spacing behavior on hare movements, survival, and reproduction then, should help to

decide between these two hypotheses. In this study I have examined snowshoe hare movements and spacing behavior, particularly that of juveniles and adult females. I chose juveniles because Keith and Windberg (1978) found that changes in their survival rates were most influential in overall changes in hare numbers. Females were chosen because I felt they would be most influential in determining overall reproductive rates which were also found to change with the cycle (Cary and Keith 1979). I was concerned with answering the following questions:

1. What is the spatial arrangement of hare home ranges and what does this arrangement suggest about snowshoe hare social organization?

2. Is the presence of adjacent females important in determining the use and location of a female's home range?

3. Do adult females influence juvenile movements and survival?

Answers to the first question will give some indication as to how hares divide up resources such as food and space. The second question is aimed at determining whether female spacing behavior is influential enough to prevent some individuals from breeding. The final question is an attempt to determine if spacing behavior can affect juvenile survival and thus be important in hare population dynamics. To answer these questions I monitored hare populations and carried out experiments from May 1978 to July 1979. The demography of these populations and results of the experiments will be provided. Finally, answers to the above questions will be discussed in the context of hare population dynamics.

2. STUDY AREA

The two main study areas, Silver Creek Control (S.C.C.) and Telemetry, were located near Kluane Lake, 240 km northwest of Whitehorse, Yukon Territory (Fig. 1) . The sites were separated by 700 meters of continuous forest and Silver Creek, a small stream that blocked hare movement between sites from June to mid-September. Another study area, Silver Creek Removal was located between the two main sites. It was only indirectly involved with this study. Animals were caught and removed from this area, thus creating a block of unoccupied habitat.

Topography in the Kluane area is highly variable. The study sites were located on level ground with shallow, old creek beds providing the only relief. To the north of Telemetry and the south of S.C.C. the land becomes more rugged and gains in elevation. The area surrounding each site will be described in more detail later.

The climate is characterized by long winters with light but persistent snow cover from November to late April. Snow depths were never more than 40 cm during the study. Temperatures are variable throughout the year with lows of -50°C in winter and highs of 25°C in summer. The sun is above the horizon for 4-6 hrs. during November-February and 18-21 hrs. in June and July.

The frost free period runs from early June to late August. New leaves and herbs begin to appear in spring from mid to late May, and the growing season ends in late August. This means hares have growing herbaceous and woody material available to them for roughly four months each year.

4

Figure 1.
    Location of study areas.
    S.C.C.-Silver Creek Control
    S.C.R.-Silver Creek Removal
    Tel.-Telemetry
    1-7 - Tower Locations

S.C.

150 M

N

S.C.C.

S.C.R.

TEL.

3   1   2   7   4

6

5
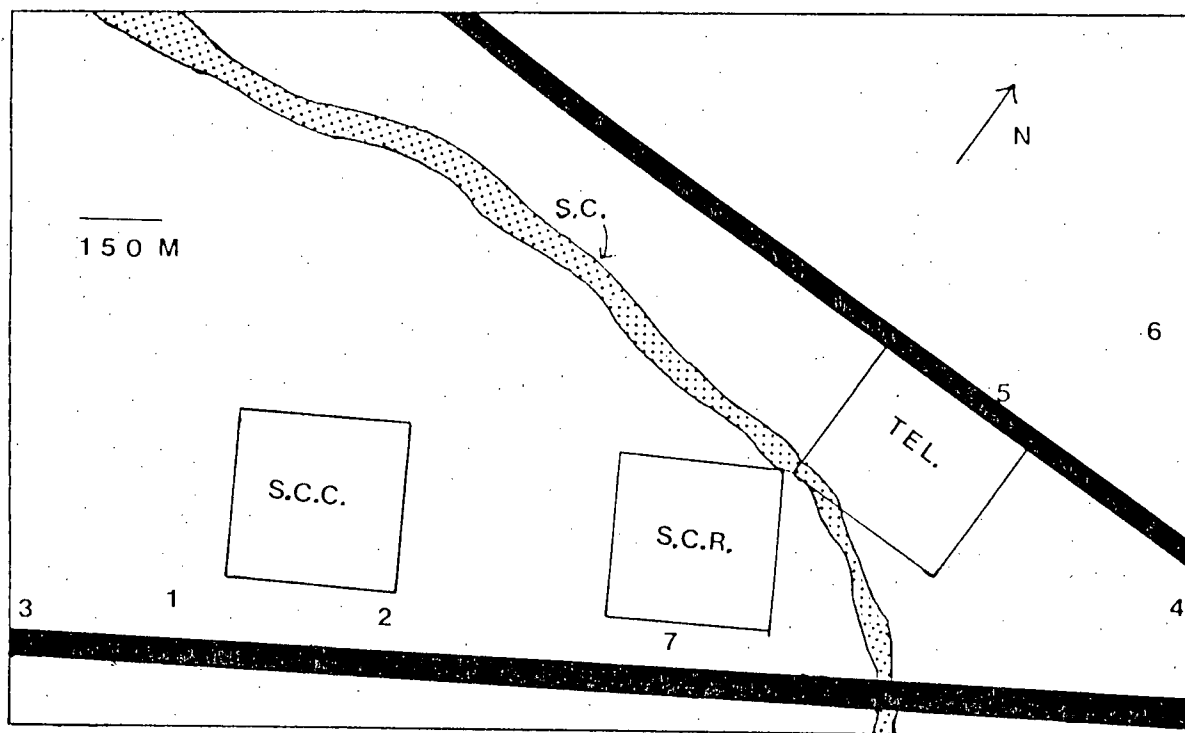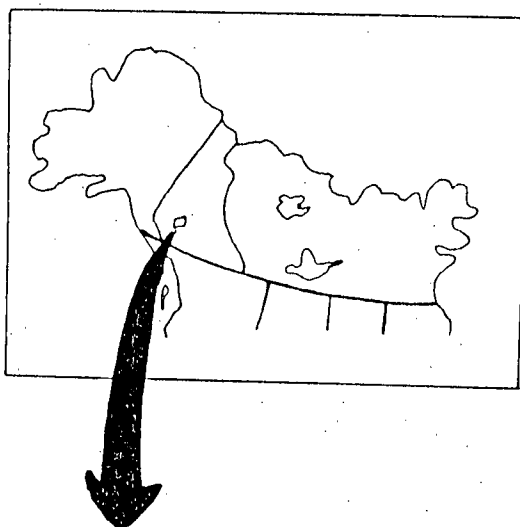
The winter of 1978-79 was unusually harsh with the coldest February on record occurring. Temperatures never rose above -30°C for the entire month. This was followed by a mild March and relatively early spring.

Vegetation in the area is northern boreal forest. It is similar to the closed spruce community as classified by Douglas (1974). White spruce (Picea glauca) is the dominant tree species with various amounts of willow (Salix spp.) and buffaloberry (Shepherdia canadensis) making up the understory. Bearberry (Arctostaphylos uva-ursi), Dryas drummondii, Hedysarum boreale and Lupinus arcticus provide much of the herbaceous ground cover.

Potential competitors of the snowshoe hare are moose (Alces alces) and Arctic ground squirrels (Spermophilus undulatus). Mammalian predators present are lynx (Lynx canadensis), coyote (Canis latrans), wolf (Canis lupus), weasel (Mustela rixosa) and (Mustela frenata) and marten (Marteo americana). Great horned owls (Bubo virginianus), goshawks (Accipiter gentilis), red-tailed hawks (Buteo jamaicensis) and Swainson's hawks (Buteo swainsoni) are the major avian predators. The above gives a general description of the study area. I will now describe the two specific sites in more detail.

2.1. Silver Creek Control

S.C.C. was located on an old rocky stream outwash. The entire area is covered by mature white spruce with a sparse

understory of willow and buffaloberry. The Alaska Highway runs along the southern edge of the area and creates an open space of 250 meters between the study area and suitable hare cover beyond. Very few animals are known to have crossed this strip. The remaining three sides of S.C.C. have habitat similar to the site itself. Silver Creek runs 300-350 meters north of the grid. However, the area up to 100 meters from the creek has a more open spruce canopy and a thicker understory of willow and buffaloberry than on the study area.

2.2. Telemetry

Telemetry is bordered on the south by Silver Creek and the north by a lightly used road. The road does not act as a barrier to movements and animals pass freely from one side to the other. The east and west sides of Telemetry are bordered by continuous forest. Vegetation on the actual study area is more variable than on S.C.C. . The north half is covered by mature spruce with a sparse understory while the southern half has a thick willow understory and open spruce canopy.

3. MATERIALS AND METHODS

3.1. Trapping

Each study area consisted of a 300 x 300 meter (9.29 ha) trapping grid. One hundred stations were arranged in a 10 x 10 pattern with 30 meters between stations. Fifty double door live traps were placed at alternate stations on each grid. If runways were present nearby, traps were placed on them. Traps were baited with alfalfa cubes throughout the study. In late May and June of 1979 this was supplemented with apples. During winter, most traps were set with a single door open and the bait well behind the treadle.

Traps were set for two consecutive nights and checked each morning. During the summer they were also checked in the evening of the first day. When not in use traps were left in position and locked open. From May through September 1978 traps were set on both grids once a week. They were also set once in mid-October, twice in late November, weekly in March 1979, twice in late April, and then weekly until the end of July. S.C.C. was also trapped once in each of August, September, and October, 1977.

The location, tag number, sex, reproductive condition, and right hind foot length was recorded for each animal captured. Newly captured animals were ear-tagged with a numbered metal tag. Reproductive condition of females was determined by the size and appearance of nipples. Medium or large nipples with matted fur indicated that the individual was nursing a litter.

Pregnant females close to term could be determined by palpation. Males with testes in scrotal sacs were considered to be in breeding conditon.

3.2. Telemetry

In mid-May of 1978, hares on both study areas were equipped with radio transmitters (Wildlife Materials Inc.). Each transmitter produced a pulsing signal at a specific frequency within the range of 150.8 to 151.8 Mhz. Each unit weighed 30 g and was attached around the animal's neck with strapping.

Radios were located with a receiver attached to a directional yagi antenna. Strongest signal reception occurred when the antenna was pointed directly at the transmitter. In the initial stages, during late May and early June 1978, radio-tagged animals were located by means of a small portable handheld antenna. The direction of strongest signal strength was followed until I was certain of the animal's location. For the rest of the study, the majority of animals were located by use of permanent towers. Two or more of these were established near each grid and their relative locations are shown in Fig. 1. Towers 1, 2, 4, and 5 were established in mid-June 1978. Tower 3 was established in late August 1978 while 6 and 7 were erected in May 1979. Towers 1 and 2 were 12 meters high while 6, 7, 3, and 4 were five meters high. The latter two, however, were placed on high points of land to increase their range. Radios could be detected at a distance of up to two km with these permanent towers.

Each tower supported a directional yagi antenna that could be rotated from ground level. The direction of the antenna was read off a protractor at the base. Positions of radio-tagged animals were determined by triangulation. The bearing of strongest signal for each transmitter was determined from two towers. The point at which these two bearings crossed indicated the transmitter's location. The location of a radio by this technique is not actually a point but a polygon shaped probability area. The size and shape of the polygon is dependent upon the location of the radio relative to the locating towers (Heezen and Tester 1967). This is due to the fact that some mechanical error exists in determining the bearing of the strongest radio signal. To determine the size of this error I placed radios at known locations and recorded the bearing to each a total of 20 times from each of the towers. The 95% confidence intervals around the means were determined and found to be near 3° each time. I took this to be the error of the system. In other words a 3° band centered around the recorded bearing would contain the true bearing 95% of the time. If a 3° band is drawn from each of two towers as shown in Fig. 2 the lines meet to form an error polygon (Heezen and Tester 1967). This polygon changes in size and shape depending on where the lines meet relative to the towers. For example, compare the error polygons at points A and B. That at position A has a much shorter length relative to that at position B.

During the study, radios were located from tower combinations that minimized the length of the error polygon. Radio locations falling in an area where the error polygon

Figure 2.
 Changes in error polygon length (EPL) produced by a
 telemetry system having a 3º error (3º confidence interval
 - C.I.). Notice EPL changes with its position relative to
 the locating towers (A vs. B).
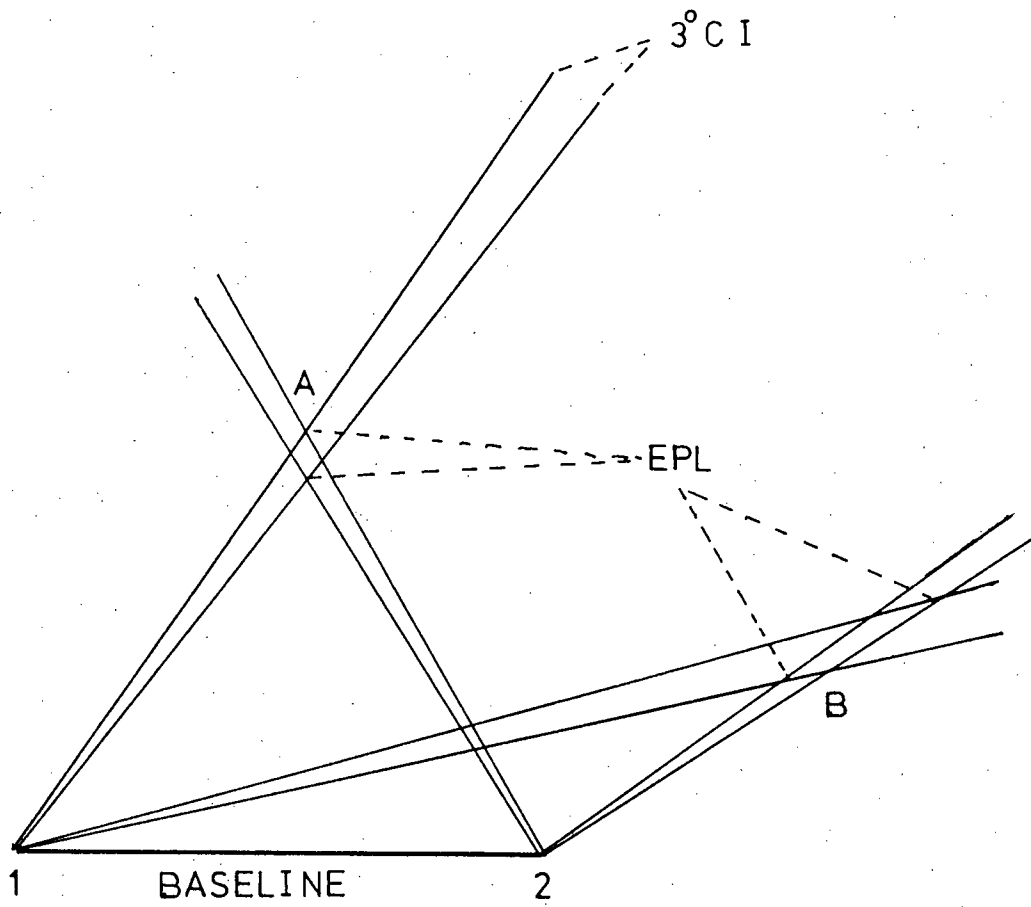
length was greater than 150 meters were disregarded.

When possible, each transmitter was located synchronously by two people, one at each of two towers. However, in most instances, a single person located all of the transmitters in the area before moving to the next tower to repeat the process. This meant that a maximum of 15 minutes could occur between the taking of the first and second bearings on each animal.

Rapid variations in transmitter signal strength are produced when an animal changes its orientation relative to the receiving antenna. These changes were used to determine whether the animal was active or not. Individuals that showed no activity or changes in location over 2-3 days were then located with a handheld antenna to see whether the animal was dead or if the transmitter had fallen off. This was also done for any animals making unusual movements. Transmitters found in this way were examined to determine what had happened to the owner. If a portion of the animal still remained the proximate cause of death could often be determined. If only the radio was found and the strapping was still intact I could be sure that the animal was dead. When the strapping was missing or broken the owner's status was recorded as unknown.

Locations of radio-tagged animals were taken at various times and frequencies throughout the study. These will be specified where pertinent. In late July of 1978 the first juveniles were radio-tagged. No animals were tagged below a weight of 500 g.

The above provides a description of general methods used during the study. More specific techniques will be provided at

the beginning of relevant sections.

4. DEMOGRAPHY

This section examines the demography of hare populations on Telemetry and S.C.C. . Trapping estimates of population density will be provided along with survival rates from both trapping and telemetry techniques. The number of young produced in each area will also be estimated. Finally, the values obtained will be compared to those of previous studies.

I used two mark-recapture techniques to estimate numbers. They were: complete enumeration (Krebs 1966) and the Jolly stochastic model (Jolly 1965). As the name suggests complete enumeration involves capturing all of the animals present during each trapping session. The Jolly method is based on multiple capture data which is used to generate probability values of survival and population growth. These in turn are incorporated into a model which produces population estimates. Both estimation techniques are sensitive to the trappability of the animals involved. The Jolly method assumes that all individuals in the population have equal probability of capture while complete enumeration is effective only when the trappability of animals is greater than 50% (Hilborn et al. 1976).

To determine whether these criteria were met I measured the trappability of the population at different times. Trappability for each animal was calculated by the formula:

$$\frac{(\text{number of captures during time t}) - 2}{(\text{maximum potential number of captures during time}) - 2}$$

An example would be as follows. Over six trapping sessions in time t an animal was first caught in session numbers 1 and then again in 3, 4, and 5. The total number of captures over time t was 4. The maximum potential number of captures was 6. Subtracting first and last captures gives a trappability value of 2/4 or 50%. Values for each animal were then averaged to give a mean for the population. Subtracting 2 from the numerator and denominator excludes animals that are captured only once or twice (Hilborn et al. 1976).

4.1. Results

4.1-1. Trappability

Table 1 shows that mean trappability was less than 50% in Oct. 78 - Feb. 79 and May-June 1979 on Silver Creek Control. Values though, were never less than 40%. In three of five time periods examined, animals were less catchable on S.C.C. than on Telemetry. Trappability varied between sexes. Major differences were apparent in March-June 1979 on Telemetry and Aug.-Sept. 1978 on S.C.C.. Males were highly trappable in March and April 1979 on both grids. Average trappability over the entire study was 59% on Telemetry and 53% on S.C.C..

Hilborn et al.(1976) found that complete enumeration underestimated population size by at least 20% when trappability dropped below 50%. Consequently both Jolly and complete enumeration estimates will be provided for comparison. Any differences between estimates may indicate biases that can be

TABLE 1

Trappability of animals on Telemetry and S.C.C.. All values
are expressed as percentages. Sample sizes are in brackets.

PERIOD	NO. TRAPPING SESSIONS	TELEMETRY			S.C.C.		
		M	F	MEAN	M	F	MEAN
May- July/78	8	67.7(7)	69.6(6)	68.6	74.0(3)	40.0(6)	51.0
Aug- Sept/78	5	55.2(16)	53.8(13)	54.6	40.2(11)	66.2(18)	56.3
Oct- Feb /79	6	62.9(18)	62.5(10)	62.8	48.3(11)	44.4(14)	46.1
Mar- Apr /79	4	86.5(13)	53.0(11)	71.2	85.2(9)	70.4(9)	77.8
May- June/79	6	69.2(13)	41.7(14)	55.0	39.4(11)	48.3(10)	43.7
May/78- July/79	28	59.3(36)	59.0(38)	59.6	52.2(26)	54.2(26)	53.5

corrected for.

4.1-2. Changes in Numbers

Fig. 3 shows that M.N.A. (minimum number alive)
estimates were similar for the two study areas. Numbers began to
increase in 1978 with the recruitment of juveniles into the
population. This occurred in early July on both grids but at a
slower initial rate on Silver Creek Control. After numbers
peaked in September there was a moderate drop in October and
subsequent recovery in November. In early March 1979 the
population had dropped to half that present in September.
Immigration, primarily by females, in early May, caused an
increase in estimates. Estimates in June were 1.9 and 2.6 times
those of one year earlier on S.C.C. and Telemetry respectively.
The M.N.A. estimate for August 1977 on S.C.C. was 4. Fig. 4
shows that Jolly population estimates followed a pattern similar
to M.N.A. but are up to 20 % higher. Hare numbers then, were
increasing during 1977-1979. Both grids followed similar
patterns of density change.

4.1-3. Initiation of Breeding Season

Trapping did not begin early enough in 1978 to determine
when males came into breeding condition. All adult males
captured between May 1 and August 7, 1978 were scrotal. All were
in non-breeding condition after mid-August.

Figure 3.
    Minimum number alive (M.N.A.) estimates for S.C.C. and
    Tel. during the study.
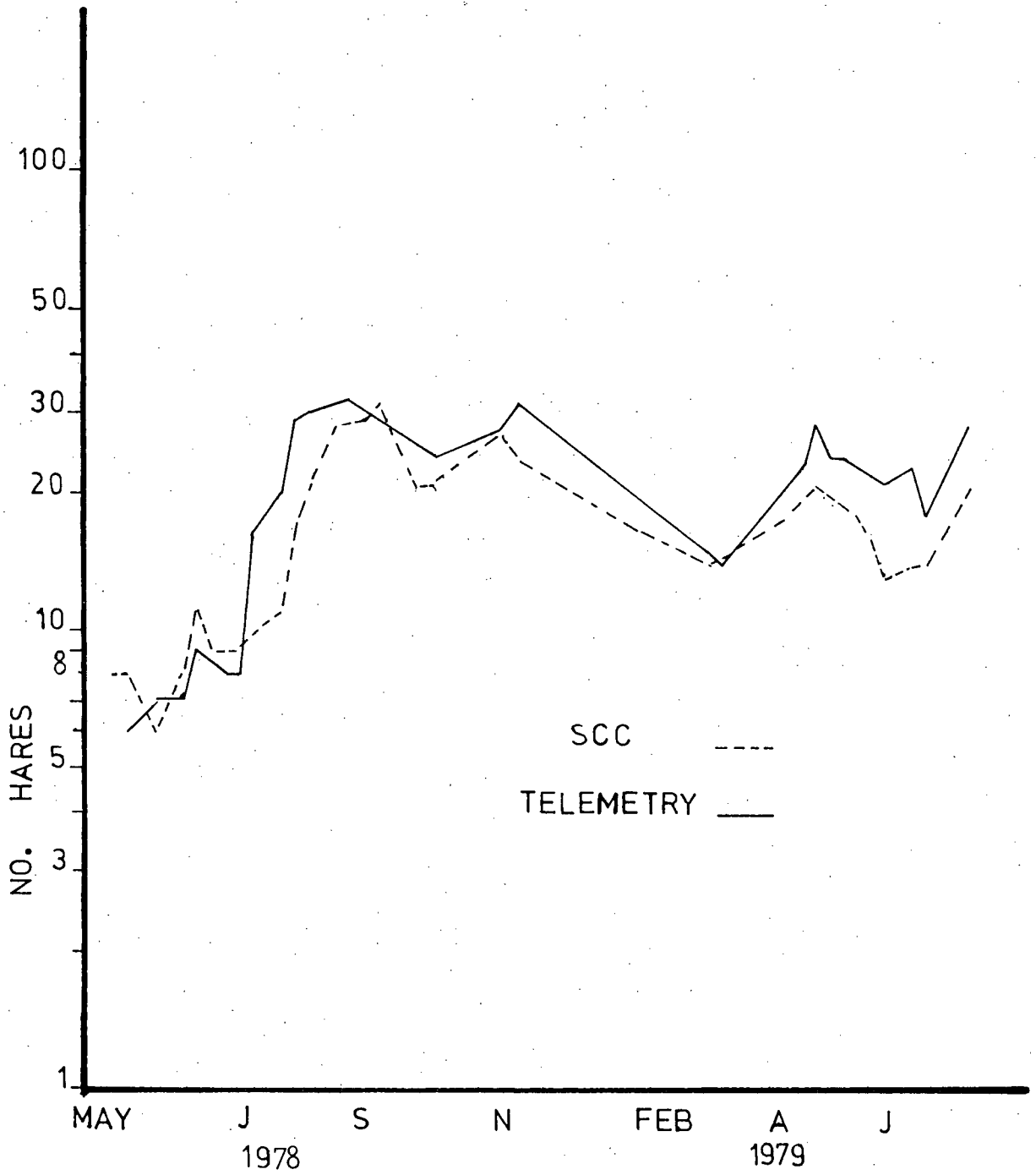
Figure 4.
     Jolly population estimates for S.C.C. and Tel. during the
     study.
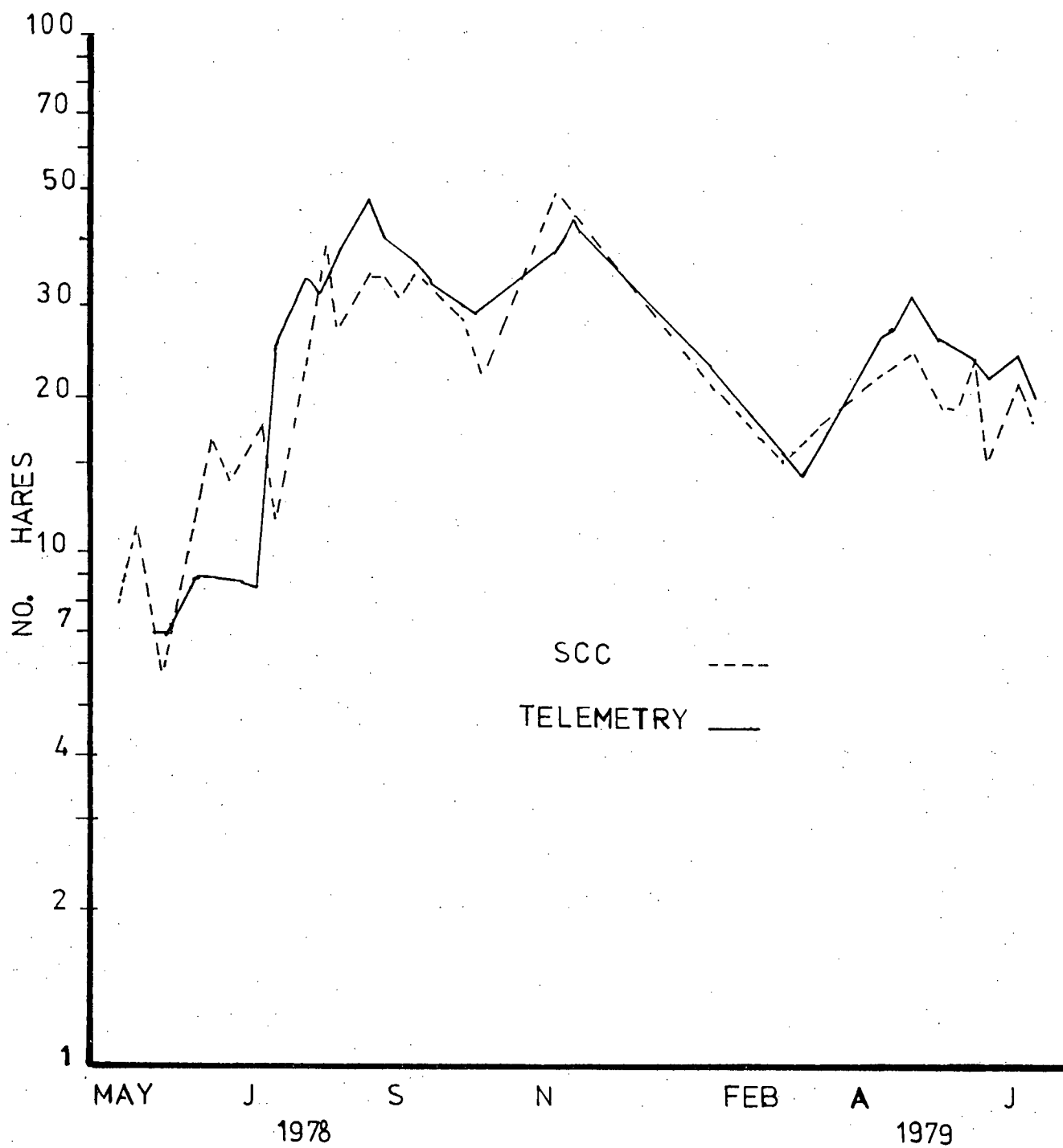
In 1979, four of 15 males captured during March 6-8 were scrotal. Two weeks later 20 of 23 were classed as scrotal and the three abdominal animals continued to be so even in late June, suggesting that they did not breed. Thus half of the males were in breeding condition by March 15,1979.

The first litters of 1978 were born between May 25 and June 3, and four of six S.C.C. females caught on May 28 were lactating while a fifth was four days later. The final female was lactating when it was next captured on June 12. All females on Telemetry were lactating by June 3. Thus a gestation period of 37 days (Severaid 1942) would put first litter conception dates in 1978 around April 23. Final litters were born in early August and females had ceased lactating permanently by September 23.

In 1979 first litters were born around May 19. Two females removed from Telemetry and placed in 3 x 9 m pens gave birth at this time. Two pregnant females which died while being live-trapped on May 17-18 had embryos weighing over 50 g indicating that they were close to term. Four of eight females caught on S.C.C. during the week of May 21-27 were lactating. The remaining four were lactating the next week.

On the Telemtry grid two females had given birth during the week of May 14-20, 1979. Two weeks later all but two females captured were lactating. It appeared, through later trapping, that these two animals did not produce a first litter.

To summarize, first litters in 1979 were born between May 18 and June 3. This places first litter conception dates at April 11, almost two weeks earlier than in 1978.

4.1-4. Number of Young

Meslow and Keith (1968) found that births of litters were highly synchronized. This, along with immediate postpartum mating, served to produce distinct litter groups distinguishable by weight. Three litters were born on both Telemetry and S.C.C. in 1978. First trapping dates of individuals from respective litters were June 22, July 19, and August 18 on Telemetry. Second and third litter young were captured 10 days later in each case on S.C.C.. Young started to enter traps around roughly 25 days of age and at a weight of 300-400 g. Adult females were not caught often enough to determine whether each individual produced three litters.

The number of young caught from each litter and each grid is shown in Fig.5. Numbers are determined from young caught before Sept. 30. After this time trapping was not frequent enough to place newly tagged juveniles into their respective litter groups. Numbers of young caught per litter were similar on each grid except for litter two where the number was 50% higher on Telemetry. The second litter produced as many young as the first and third litters combined. The difference in number caught between first and second litters may be explained by larger litter sizes in the latter as found by Cary and Keith (1979). This cannot explain the difference between litters two and three however, as Cary and Keith (1979) found litter sizes and pregnancy rates similar for the two. The total number of young trapped to September 30 was 49 on Telemetry and 37 on S.C.C.. This produced a juvenile/female ratio of 12.25 on

Figure 5.
    Number   of   young trapped in 1978 on S.C.C.   and Telemetry.
    Notice that over half of the animals were from   the   second
    litter.
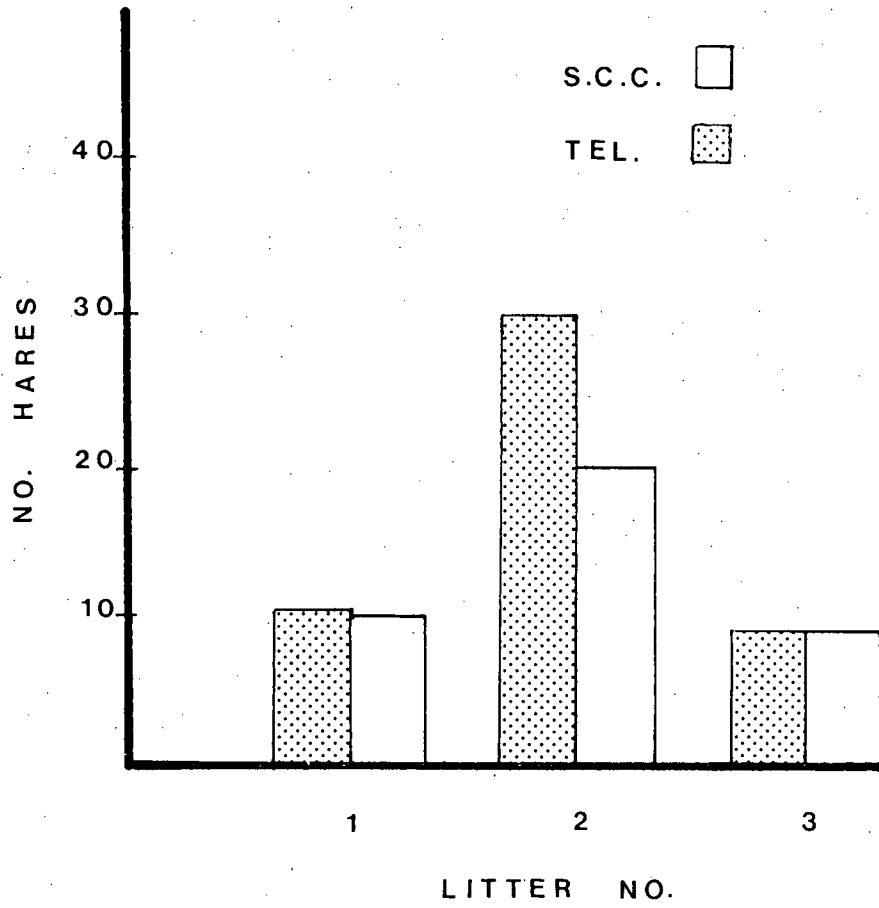
Telemetry as compared to 6.3 on S.C.C.

To summarize, over half of the juveniles captured were from the second litter. Twice as many juveniles were caught per female on the Telemetry grid as on S.C.C..

4.1-5 Survival

Survival estimates were calculated in three different ways. They were:

1. Trapping method - this method uses recapture data to calculate the ratio of

$$\frac{\text{(number of animals released at time t and known to be alive at t + 1)}}{\text{(number of animals released at time t)}}$$

2. Simple telemetry - This technique records the number of animals known to be alive at time t, as determined by telemetry and then records how many of these are still alive at time t+1. It is similar to the trapping method except that a radio-tagged animal located and considered to be alive is equivalent to an animal being released after trapping.

3. Trent and Rongstad (1974) - This technique uses telemetry to calculate a mean daily survival rate (Sd) by the formula:

Sd = (x-y)/x where:

x = number of radio-hare days (1 radio-hare day is equal to 1 radio-tagged hare in the field for 1 day) in time

period t.

y = number of mortalities in time period t. Survival over n days can be determined by (Sd) and confidence limits can be placed on the estimate by following the method of Trent and Rongstad (1974).

Telemetry is useful as a method of measuring survival only if radio-tagged animals survive as well as untagged individuals. Few studies have attemped to determine if this is true (Herzog 1979; Boag et al. 1973). Brand et al. (1975) showed that overwinter weight loss of hares was similar in collared vs. uncollared hares. However, sample sizes were small. As well, radio-tagged animals which die over the winter may still lose weight at a greater rate than untagged individuals and thus suffer higher mortality rates. This could not be detected by looking at weight losses of survivors.

To test for equal survival I compared the trapping survival of radio-tagged animals with those that were not tagged. Because the majority of the animals were radio-tagged at some point during the study it was difficult to obtain a large sample of untagged animals. I overcame this by examining the survival of all individuals captured for the first time between July 1 and December 1. These were divided according to whether or not they had received radio collars. Finally I calculated how many of these individuals were still alive May 1, 1979.

Trapping survival of radio-tagged animals was higher than for untagged individuals. None of 25 animals on S.C.C. without collars survived to May 1. Five of 21 with collars survived. On Telemetry 3 cf 43 without collars survived whereas 5 of 22 with

collars survived. Although this suggests that collars did not increase mortality rates, it is not completely satisfactory. Animals that received radios were most often those being captured regularly on the grid. As a result most untagged animals in the sample were captured only once or twice, thus biasing the sample toward individuals with high rates of early disappearance.

To test further whether radio-tagged and untagged hares had similar survival rates I examined survival of individuals on another trapping grid with no radio-tagged hares. This grid (1050) was located two km east of the main study areas. It consisted of a trapping grid arranged similarly to S.C.C. and Telemetry. Animals were trapped every three weeks throughout the summer and most of the winter. Fig. 6 shows that survival of radio-tagged hares on S.C.C. and Telemetry was always equal to or greater than those merely live-trapped on 1050. This too, suggests that radio-tagged hares had survival rates comparable to untagged animals.

Fig. 7 compares survival rates as determined by the three methods previously described. Animals from both grids were combined. Juveniles and adults were pooled since there were no significant differences in survival between the two groups. Trapping estimates were always lower than either of the methods using telemetry. The difference between the trapping and telemetry estimates was significant in Nov. - Feb. and May - June 1979 (X^2; $P < .05$). Survival estimates by the two telemetry methods were very similar. Because of this, for the sake of brevity, only the simple telemetry method will be

Figure 6.
     Monthly survival rates determined by trapping on 1050, a
     grid where no animals were radio-tagged, and S.C.C. and
     Telemetry, grids where a large portion of animals were
     radio-tagged. Notice survival rates on S.C.C. and
     Telemetry were equal to or higher than those on 1050.
     Sample sizes are placed above each column.
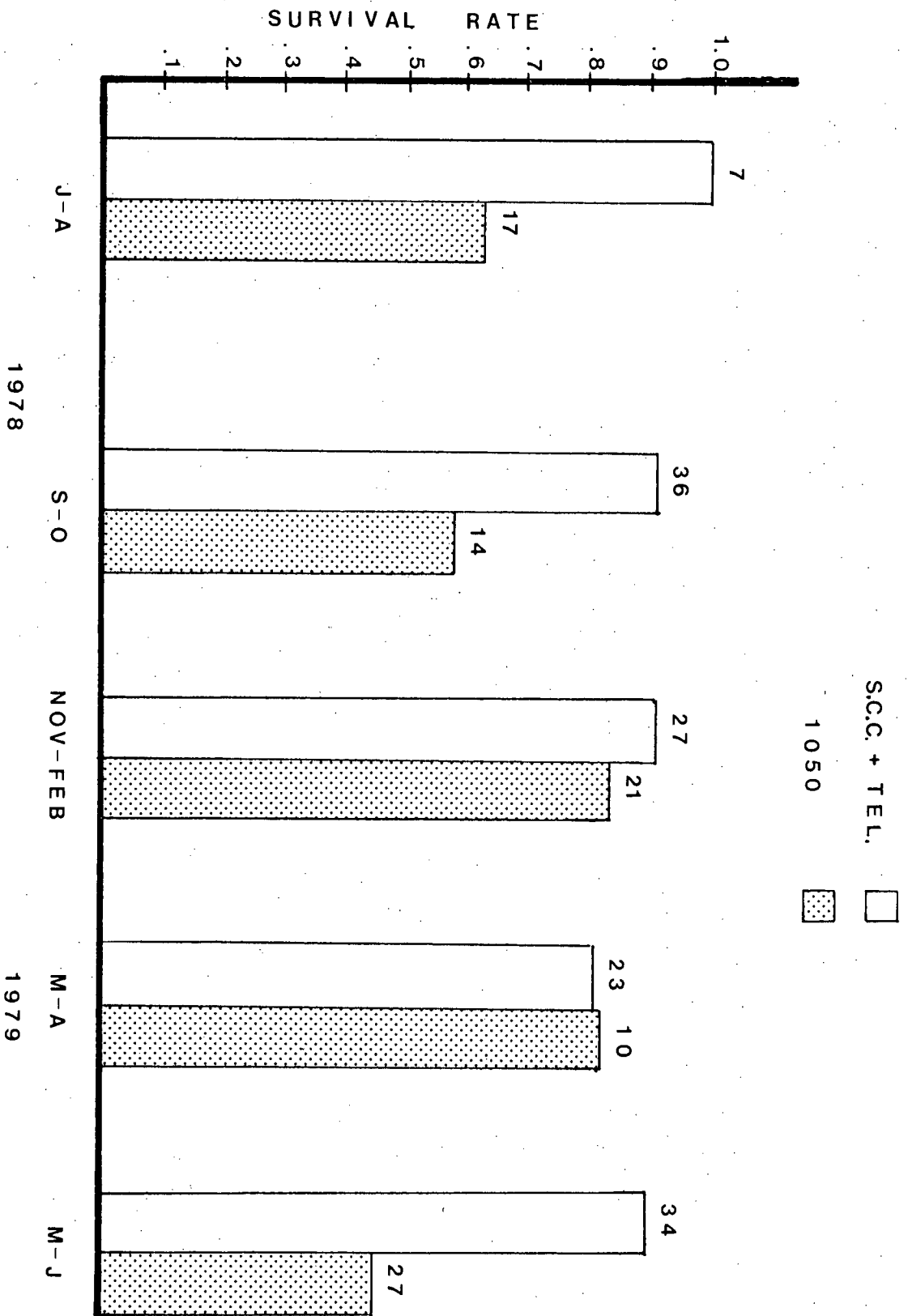
Figure 7.
Comparison of monthly survival rates as determined by
trapping and telemetry (two methods). Grids have been
combined. Notice that trapping rates are much lower than
telemetry estimates in Nov.-Feb. and May-June 1979. Sample
sizes are found at the top of each column. Trent and
Rongstad (1974) sample sizes represent radio-hare days.
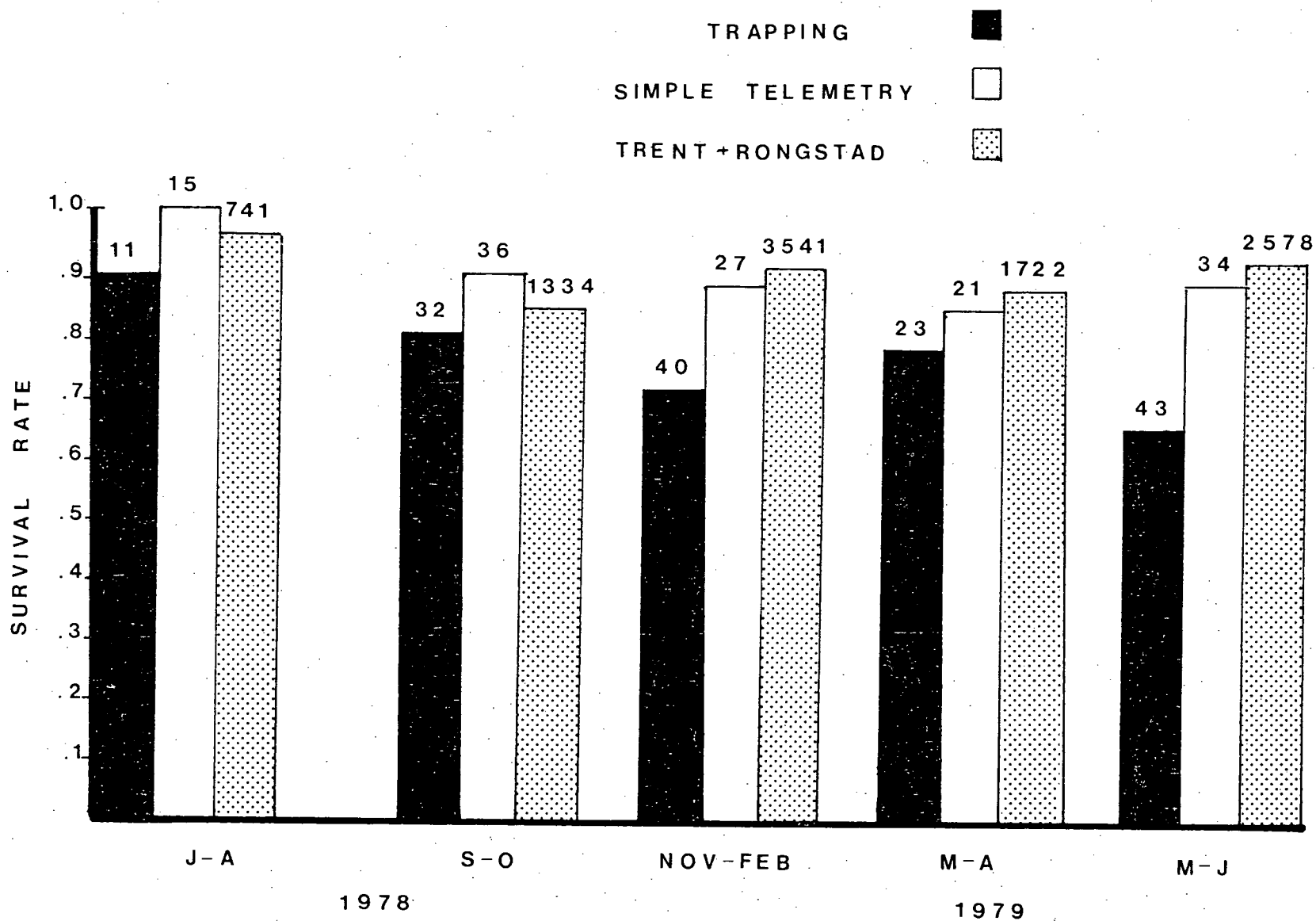
discussed from now on.

Fig. 8 shows that monthly telemetry survival estimates were similar for the two grids throughout the study. Rates were lowest in March - April 1979 and highest in July -August 1978 but the differences were not significant (X^2; P>.05). No losses were recorded until September at which time survival dropped by 10%. It continued to remain near 90% per month for the duration of the study. In contrast to telemetry survival rates Fig. 9 shows that monthly trapping survival estimates averaged 15% lower on S.C.C. control than on Telemetry. The largest differences occurred in May-June of each year.

To summarize, monthly survival during the study was fairly constant with levels slightly lower in March - April 1979. Survival estimates by trapping and telemetry differed in Nov. - Feb. 1978 and May - June 1979 by 17% and 24% respectively. The difference in May - June 1979 was due mainly to an unusually low trapping survival on S. C.C. at this time.

4.1-6. Juvenile Survival

A number of workers have concluded that juvenile survival may be important in hare cycles (Keith and Windberg 1978; Green and Evans 1940a) and small mammal cycles in general (Krebs and Myers 1974). Table 2 shows juvenile survival rates from first trapping to May 1. The animals are grouped according to the litter they were born in. Survival of first litter young was twice that of the second. No third litter young survived. Overall juvenile survival from first trapping to spring was less

Figure 8.
     Comparison of telemetry monthly survival rates   on   S.C.C.
     and Telemetry. Note the slightly lower rates during winter.
     Sample sizes are placed above each column.
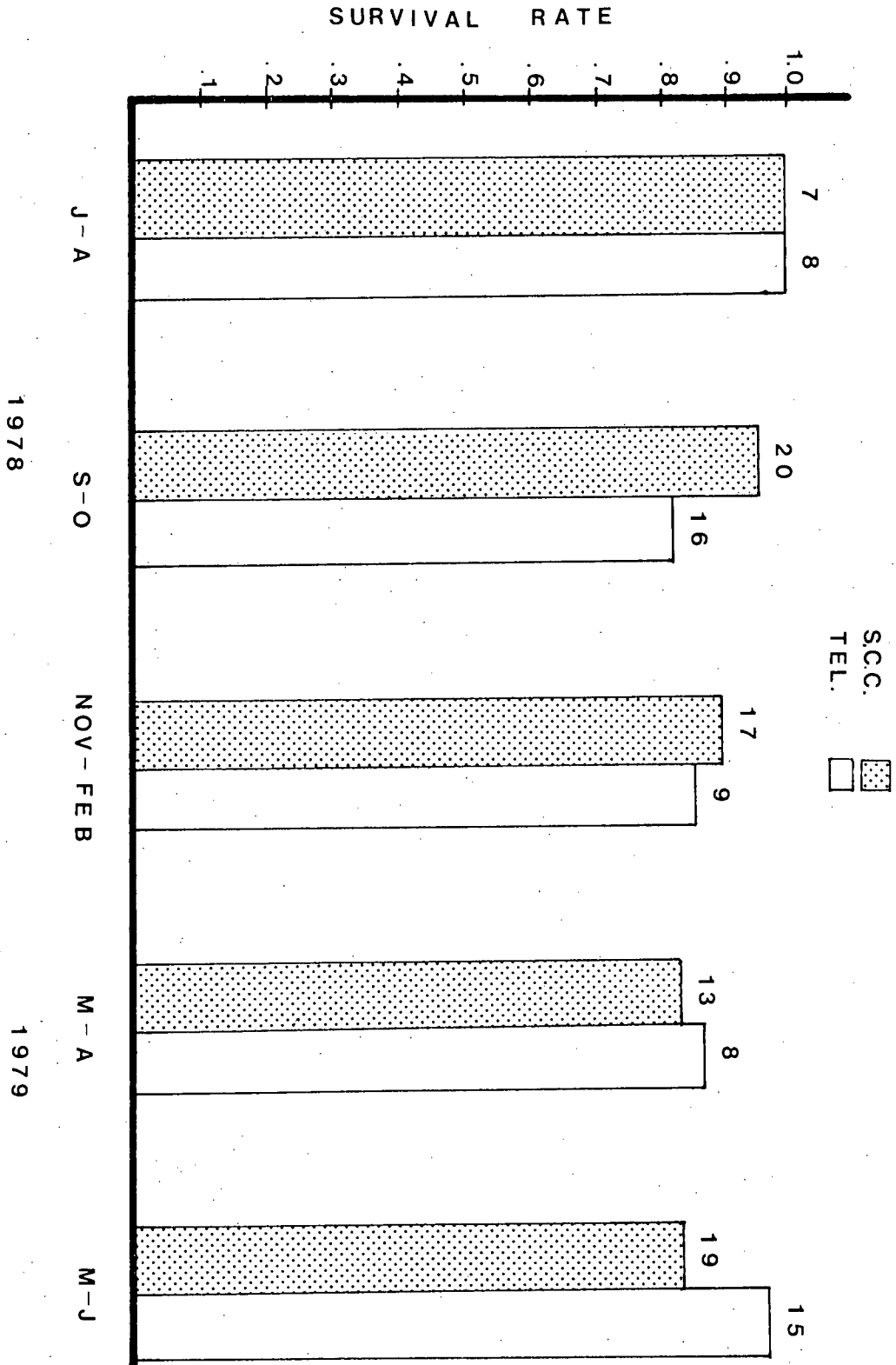
Figure 9.
    Comparison   of   monthly   survival   rates   on   S.C.C.   and
    Telemetry as determined by trapping results. Notice the low
    rates during Nov.-Feb. on both grids and on S.C.C. in
    May-June 1979. Sample sizes are placed above each column.

SURVIVAL RATE

1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1

M—J

11
6

1978

J—A

8
3

S—O

16
16

S.C.C.
TE L.

NOV—FEB

13
27

1979

M—A

11
12

M—J

19
24
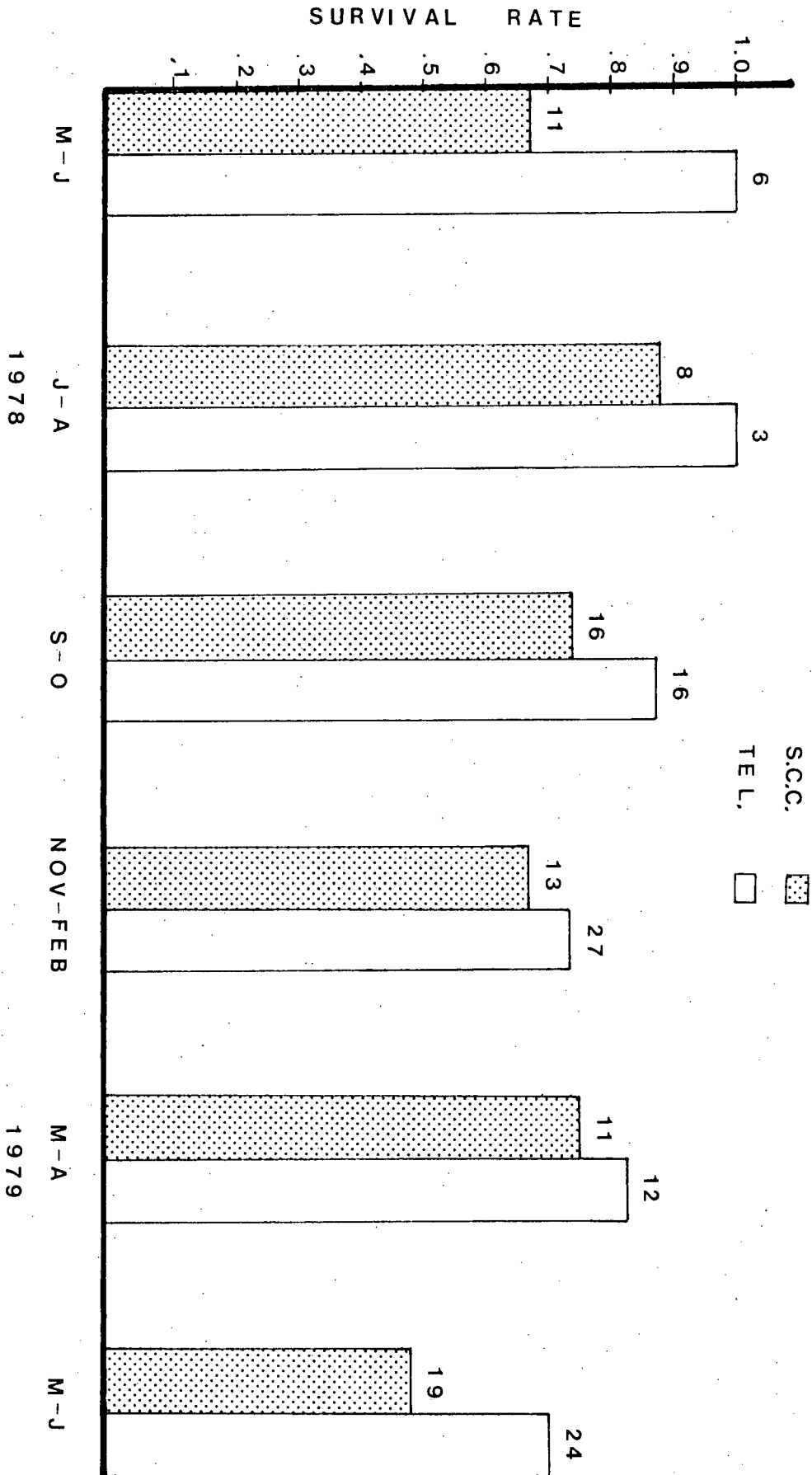
TABLE 2

Survival rates of juveniles from first trapping to May 1.
Individuals were divided according to litter group by weight
at first capture. Sample sizes are in brackets.

Litter No.	1	2	3	Total
S.C.C.	0.33(9)	0.15(20)	0.0(8)	0.16(37)
Telemetry	0.33(12)	0.17(29)	0.0(8)	0.18(49)
Combined	0.33(21)	0.16(49)	0.0(16)	0.17(86)

than 20%. This was the same as annual adult survival (2 of 10). Juvenile survival did not decrease throughout the winter as suggested by Keith and Windberg (1978). Monthly telemetry survival rates were .92 (n=23) from Sept. 1 - Dec. 1. This compares with rates of .88 (n=23) from Dec. 1 - May 15. Trapping survival rates showed similar changes.

Table 3 shows the proximate causes of death of 38 radio-collared animals. Predators were responsible for 24 of the 27 cases in which the cause of death could be determined. This figure is probably an overestimation of the effect of predation as it was sometimes difficult to determine whether animals had been predated or scavenged after they died. I tried to reduce this problem by placing finds where there was some doubt in the unknown cause of death category. Only three animals were found dead with no signs of predation. All of these occurred in early March near the end of a long continuous cold spell. The individuals were found in forms completely undisturbed. It appears that death was probably due to starvation triggered by the long period of cold temperatures (Pease et al. 1979). Four animals died because of poorly fitting collars which became lodged between their upper and lower jaws. They were unable to eat and thus starved.

4.2. Discussion

Since changes in numbers and survival rates are integral parts of the snowshoe hare cycle it is important that the values obtained accurately reflect the events occurring. The fact that

TABLE 3

Causes of death of radio-tagged hares.

Predator			Starvation	Collar Caused	Unknown
Terr.	avian	Unknown			
10	9	5	3	4	7

the changes in numbers determined by the Jolly and complete enumeration techniques were similar throughout the study support the validity of the estimates as an index of density. Hilborn et al. (1976) found that M.N.A. underestimated vole populations by 10-20%. If this amount is added to the M.N.A. estimates in this study, final values are comparable to those obtained by the Jolly technique. This too, suggests that the estimates are correct.

Survival estimates determined by trapping were always lower (up to 35%) than those from telemetry. This was due to two factors. Firstly, trapping cannot differentiate between death and emigration. An animal leaving the grid entirely or shifting its home range so that its chances of capture are low will appear to have died. Secondly, telemetry estimates are biased slightly high. This is because animals losing their radios and subsequently dying before being retrapped are not included in the determination of telemetry survival rates. Those that lose their collar but are retrapped before they die are included. As a result the chances of missing an animal that dies are greater than missing one that survives. This bias was small however, as only 8 of 116 radio-tagged animals disappeared with no evidence as to their fate.

Trapping survival rates were significantly lower than those determined by telemetry in the Nov. 1978 to Feb. 1979 period. This was probably due to the following. A number of radio-tagged animals were found dead in late Feb. - early March 1979. These animals died at a time three months after the last trapping session in November 1978 and one week before the first session

in March 1979. Because November was the last time of capture for many of these individuals, trapping survival would concentrate all of the losses in the Nov. - Feb. period. Telemetry estimates on the other hand, would spread them more evenly between the two periods. The end result is an underestimation of survival rates by the trapping technique in the Nov. - Feb. period.

Trapping survival rates were also significantly lower than telemetry estimates in May - June 1979. This was the result of low trapping survival estimates on S.C.C. which was caused by the following situation. Firstly, as revealed by telemetry, many animals on S.C.C. shifted their home ranges from on the grid in May to slightly off it for the duration of the summer. This movement decreased the chances of capture as shown by the low trappability of animals on S.C.C. in May - June 1979. A similar situation occurred in 1978 but high survival and a later return to the grid allowed most of the animals to be recaptured. With trapping being stopped in 1979 however, the animals were not recaptured and thus were recorded as having died. The overall result was to bias trapping survival downward in May - June 1979.

The above situations exemplify the value of telemetry as a method of estimating survival rates. Because animals do not have to be regularly trapped to supply information, behavior affecting trappability has no influence on survival rates. Telemetry survival estimates then, are unaffected by home range shifts or dispersal movements and thus present a clearer picture of survival than do trapping methods.

4.2-1. Reproduction

The earlier dates of first litter conceptions in 1979 compared to 1978 seemed to be linked primarily with the onset of spring. Snow disappeared and new growth began two weeks earlier in 1979 than in 1978. In both years first litters were born just as this new growth became readily available to the females. The linkage between onset of spring and breeding seems to be common among leporids (Meslow and Keith 1971; Cary and Keith 1979; Wight and Conaway 1961).

Results showed that during 1978 twice as many young per female were caught on the Telemetry as on S.C.C.. One possible explanation is that females on Telemetry actually produced twice as many young as those on S.C.C.. I do not think this was the case. The discrepancy was probably due to the relative spatial arrangements of animals on each grid. Radio-telemetry locations showed that females on Telemetry spent most of their time on the actual grid while those on S.C.C. spent considerably more time off in peripheral areas. As as result, there was a greater chance that juveniles on S.C.C. were born off the grid. Consequently, they had to move greater distances than their Telemetry counterparts before there was any chance of capturing them. Juveniles seem to remain fairly close to their place of birth at least until weaning (Rongstad and Tester 1971). This means there was less chance of capturing juveniles, at least initially, on S.C.C.. This explains why first captures for the respective litters always occurred 10 days later on S.C.C. than on Telemetry.

Another complicating factor may have been the presence of the removal grid (Fig. 1). This area was a block of vacant habitat relatively close to S.C.C. and Telemetry and was created by live-trapping and removal of hares. This unoccupied habitat may have influenced animals to move into this area rather than onto S.C.C. Over 40 juveniles were caught in the removal area. This was more than enought to compensate for the differences observed between S.C.C. and Telemetry.

The above factors may have caused the differences in number of young caught per adult female on each of the two study areas. If 12.25, the number of young caught per adult female on Telemetry, is taken as an estimate of average natality rates in the area, the value is relatively high. Cary and Keith (1979) provide realized natality rates of 11.3 to 16.3 young per female during increase years while Green and Evans (1940a) provide values of 6.6. Ernest (1974) found values as high as 11.7 young per female during a hare peak in Central Alaska. These figures were not computed from the number of young entering traps but from mean values of litter sizes, pregnancy rates, and adult survival. The number of young actually being caught would undoubtedly be somewhat less.

4.2-2. Changes in Numbers

Numbers doubled on S.C.C. and Telemetry from spring 1978 to spring 1979. This rate of change seems characteristic of increasing hare populations (Green and Evans 1940b; Keith and

Windberg 1978). M.N.A. and Jolly estimates remained high throughout the fall and then declined over winter. The sharp temporary decline in October was not completely due to lower survival although rates did drop from summer to Sept. - Oct.. Up to October any losses were compensated for by new individuals showing up in traps. The same was true for November. In October though, no new individuals were captured. This could have been caused by poor weather conditions during the trapping session. Freezing rain made most of the traps inoperable and decreased the catch. Because of this, the drop in October appeared larger than it actually was.

The increase in numbers in early April was also due to high numbers of untagged individuals showing up in traps. These individuals may have been present on the grid during winter or more likely, existed on the edge of the grid, and with the onset of breeding, became more mobile (Hewson 1976). This, coupled with a possible expansion of home range, may have increased the chances of capture as suggested by the high trappability of males at this time.

The decrease in numbers in May - June 1979 can, again, be only partly explained by mortality losses. The rest is due to a trapping artifact. Although many of the animals previously trapped were still alive at the end of June, as shown by telemetry survival estimates, they were not captured during the final trapping session. The population estimation techniques would then record them as dying and thus reduce population size accordingly. This results in numbers being underestimated at the end of the study.

4.2-3. Survival

An annual adult survival of 20% is relatively low for increasing hare populations. Keith and Windberg (1978) found values greater than 30% in Alberta populations. Juveniles never suffered survival rates significantly lower than adults and rates were comparable to those of other studies (Keith and Windberg 1978; Dolbeer and Clark 1975). Proximate causes of losses throughout the study appeared to be due to predation. Losses seemed to increase slightly from summer to winter, which may have been related to changes in cover and subsequent susceptibility to predation. There was very little evidence of starvation or disease.

To conclude, numbers doubled over the study even though adult survival was lower than that found in other studies. This seemed to be compensated for by higher than average natality rates. Juveniles survived as well as adults at all times. Survival rates were slightly lower in winter months and most losses had predation as their proximate cause.

5. HOME RANGE SIZE AND SPATIAL ARRANGEMENT

Home range was defined by Burt (1943) as "... that area traversed by the individual in its normal activities of food gathering, mating, and caring for young." The way these activities are performed in turn, determines the type of social organization experienced by that individual. Consequently, knowing such things as the size, location, and spatial arrangement of the home ranges of a group of individuals should provide some information as to their social organization. This concept is particularly important in species like the snowshoe hare where it is difficult to observe behavioral interactions directly. With the development of radio-telemetry it is relatively easy to obtain an accurate measure of the position of a number of hares' hcme ranges. This section presents data on the spatial arrangement of snowshoe hares monitored during the study and discusses its relevance to the animals' social organization.

5.1. Methods

Home ranges were determined by the convex polygon method (Mohr 1947) which joins the outermost locations where an animal is found to form a convex polygon. I modified this technique to include only 90% of the total number of points. Locations which were furthest from all others were discarded. This was done to exclude locations representing brief long

distance forays outside an animal's normal area of use (Burt 1943).

Animal locations were determined by radio-telemetry. As explained previously, a radio-location has associated with it, an error polygon whose length provides some index of the accuracy of the location. This length is a function of the telemetry system error and the transmitters' location relative to the locating towers. Heezen and Tester (1967) have shown that the size of a home range is affected by the accuracy of the points involved. To see how the error of my telemetry system affected home range size I performed the following analysis.

Points were placed at various position on a map. These were used as centres of hypothetical square home ranges having an area equal to 3 ha. One of these ranges can be seen in Fig. 10. When using the convex polygon method the size of a home range is affected most by the outer locations which form the actual boundary. In turn, the error involved in estimating these outer points will be most influential in overall home range size error. To obtain an estimate of this effect I determined the bearings of each corner from two locating towers (Fig. 10). Five bearings for each corner were generated by computer from a normal distribution with a mean equal to the actual corner bearing and a 95% confidence interval of 3 (telemetry system error = 3°). Bearings from each tower were combined to give five locations for each corner. They are represented by the black dots in Fig. 10 and in effect, mimic the range of locations a telemetry system with a 3° error would produce when locating an animal on the boundary of its home range. When

Figure 10.

    Method used to determine the effect of telemetry system
error (3°) on estimated home range size.

AB Error Polygon Length

Actual

Estimated

1   baseline   2
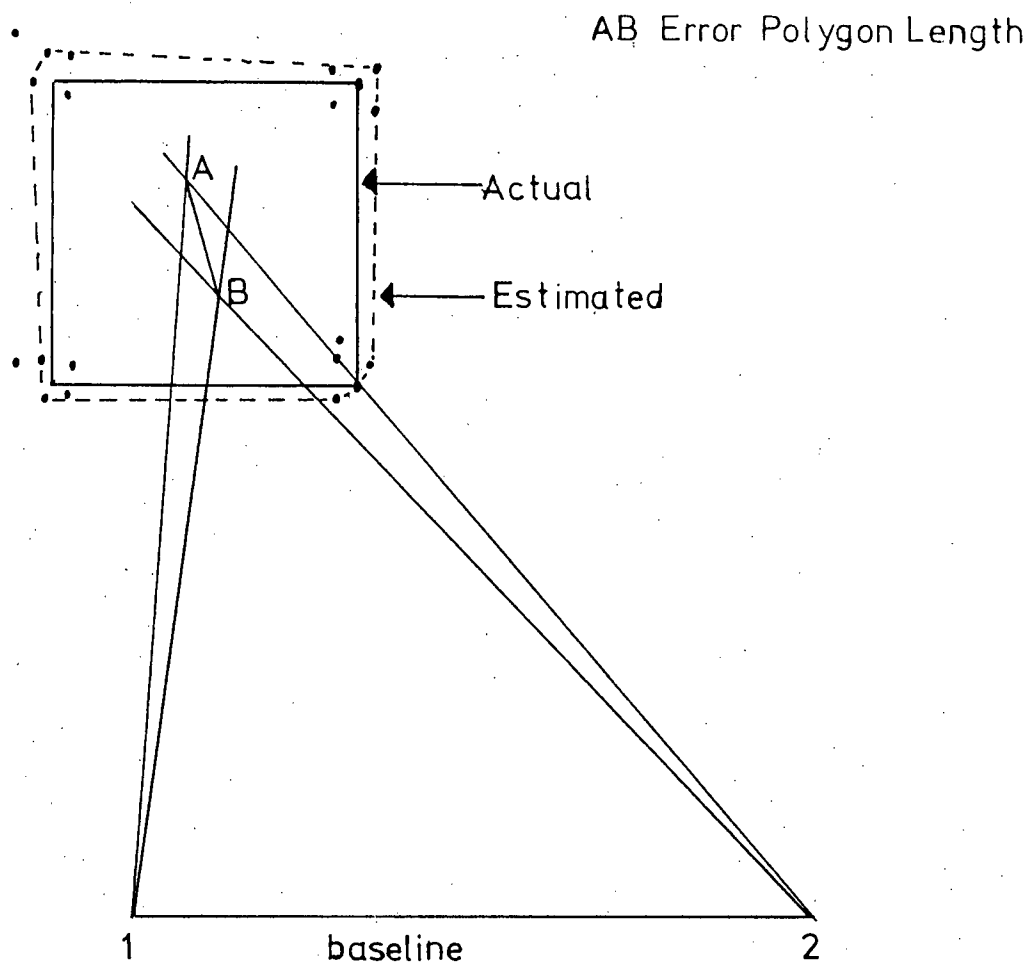
combined to produce a 90% home range these points will give an estimate of the actual range.

The error in estimating home range area (i.e. radio location estimate - actual area) is a function of where the home range is situated relative to the baseline of the two towers (Fig. 10). An index of this location is the length of the error polygon of the radio locations which is represented by AB in Fig. 10. The error polygon is smallest when the home range is at 45° from each of the towers and increases in length when the range deviates from this position.

To predict and therefore correct the error in home range area, I plotted a home range error factor:

(Estimated area - Actual area)

(Estimated area)

against AB, the error polygon length (Fig. 11). AB is the independent variable since it can be calculated for any position relative to the towers from the known 3° bearing error. Estimated area was always greater than actual area and as error polygon length increased so did the overestimation or error factor. To correct home range sizes of animals monitored during the study I determined the error polygon length associated with the home range location and used the regression equation in Fig. 11 to calculate the appropriate error factor. Estimated home range size was then multiplied by (1-error factor) to obtain the corrected size.

Error polygon lengths below 75 m were not used in the calculation of the regression. When lengths below this level

Figure 11.
    Relationship   between   error   polygon   length   and
    overestimation of home range size.
    E = estimated range size
    A = actual range size.

ERROR POLYGON LENGTH (m)
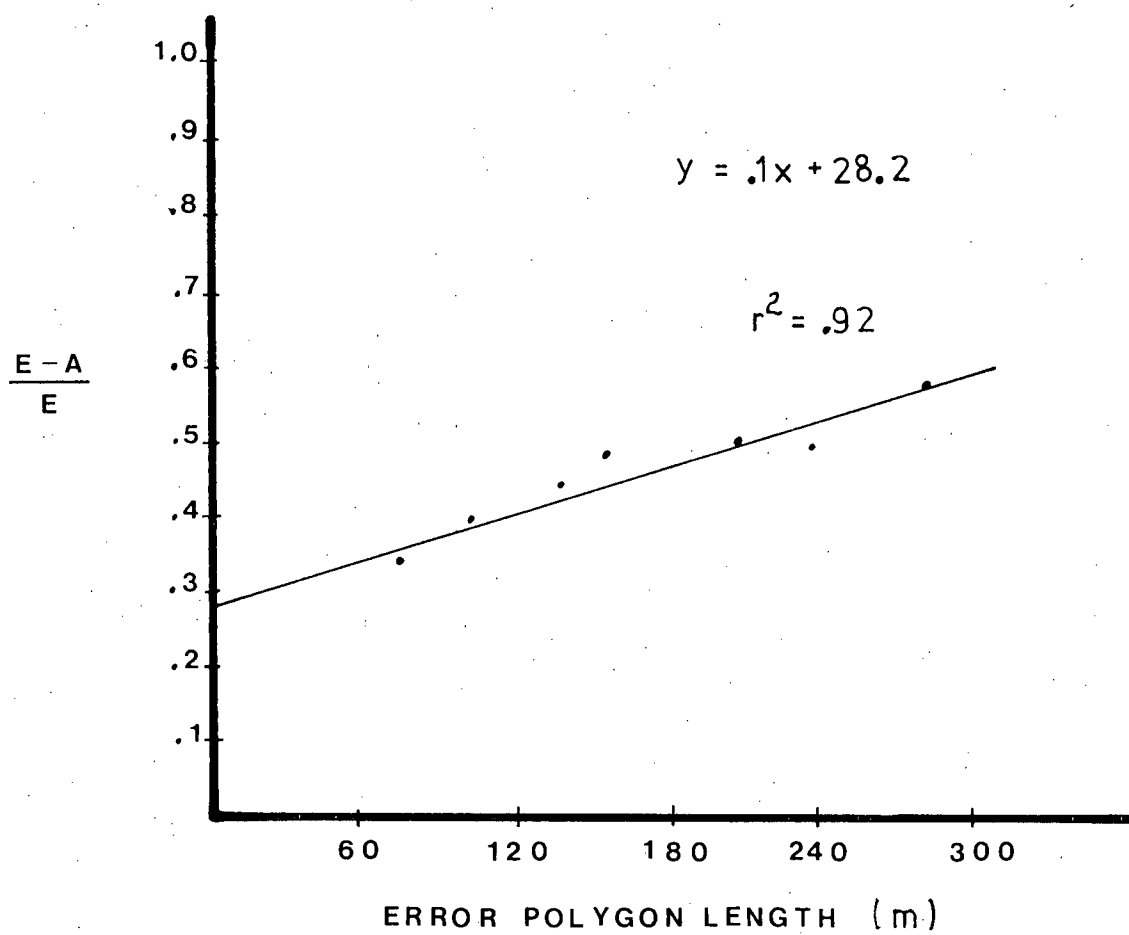
were included it was found that the relationship between error polygon length and the error factor was much poorer ($r^2=.65$). This may be due to the following situation. Heezen and Tester (1967) found that estimated home range areas remained equal to actual range size until error polygon length reached a certain size. After this, estimated ranges showed increasing over estimations in a fashion similar to this study. There appears to be an inflection point then, 75 m in this study, below which error polygon length is not related to home range size error. Consequently, I used the regression equation shown in Fig. 11 to correct the size of animals' home ranges which fell in regions with error polygon lengths greater than 75 m and less than 150 m. Those in areas with greater error were discarded because it was felt that the error involved was too great to estimate even the centre of the home range with any accuracy. Home range sizes of animals in areas where the error polygon length was less than 75 m were left unchanged. All animals on Telemetry were in this category as well as over 50% of those on S.C.C..

The percentage overlap between animals' home ranges were determined in the follcwing manner. The estimated 90% home ranges for all animals in an area were drawn on a map. The proportion of radio-locations for animal (x) found inside the area defined by all other animals' home ranges was taken as the percentage overlap for animal (x). Values were determined for each animal in this manner and averaged. Overlap by a single individual was considered the same as overlap by two or three animals.

5.2. Results

5.2-1. Home Range Size

Fig. 12 shows the 1978 monthly home range sizes of male and female hares radio-tagged on the two study areas. Home ranges were slightly smaller on Telemetry as compared to S.C.C. but the two grids were combined to increase sample size. Male home ranges averaged 25% larger than females. Fig. 13 shows monthly home ranges of radio-tagged animals in 1979. Grids have been separated because range size differed on the two areas. In all cases except July animals on Telemetry had smaller ranges. The differences were signficant for males in May and June (P<.01) and for females in June (P<.001). Males had significantly (P < .01) larger home ranges than females in all cases except on the Telemetry area in May. Home range size appeared similar in breeding and non-breeding seasons. Female home ranges averaged 25% smaller in 1979 as compared to 1978. Average female home range size varied from 3-5 ha while that of males varied from 4-8 ha. These figures are similar to those found in other studies (Bider 1961; Adams 1959, O'Farrell 1965).

Rongstad and Tester (1971) found that female hares contracted their home range size just prior to parturition. To see if this occurred in my study I compared home range size for the two week period centred around each birth with the two week period midway between births in 1978, while in 1979 I reduced this to weekly intervals. In each case the number of locations used to determine home ranges for birth and interbirth periods

Figure 12.
    Mean monthly home range sizes of radio-tagged hares in 1978
    showing   that   males   have   slightly   larger   ranges   than
    females. Narrow bars represent 95% confidence limits.
    Sample sizes are placed above each column.
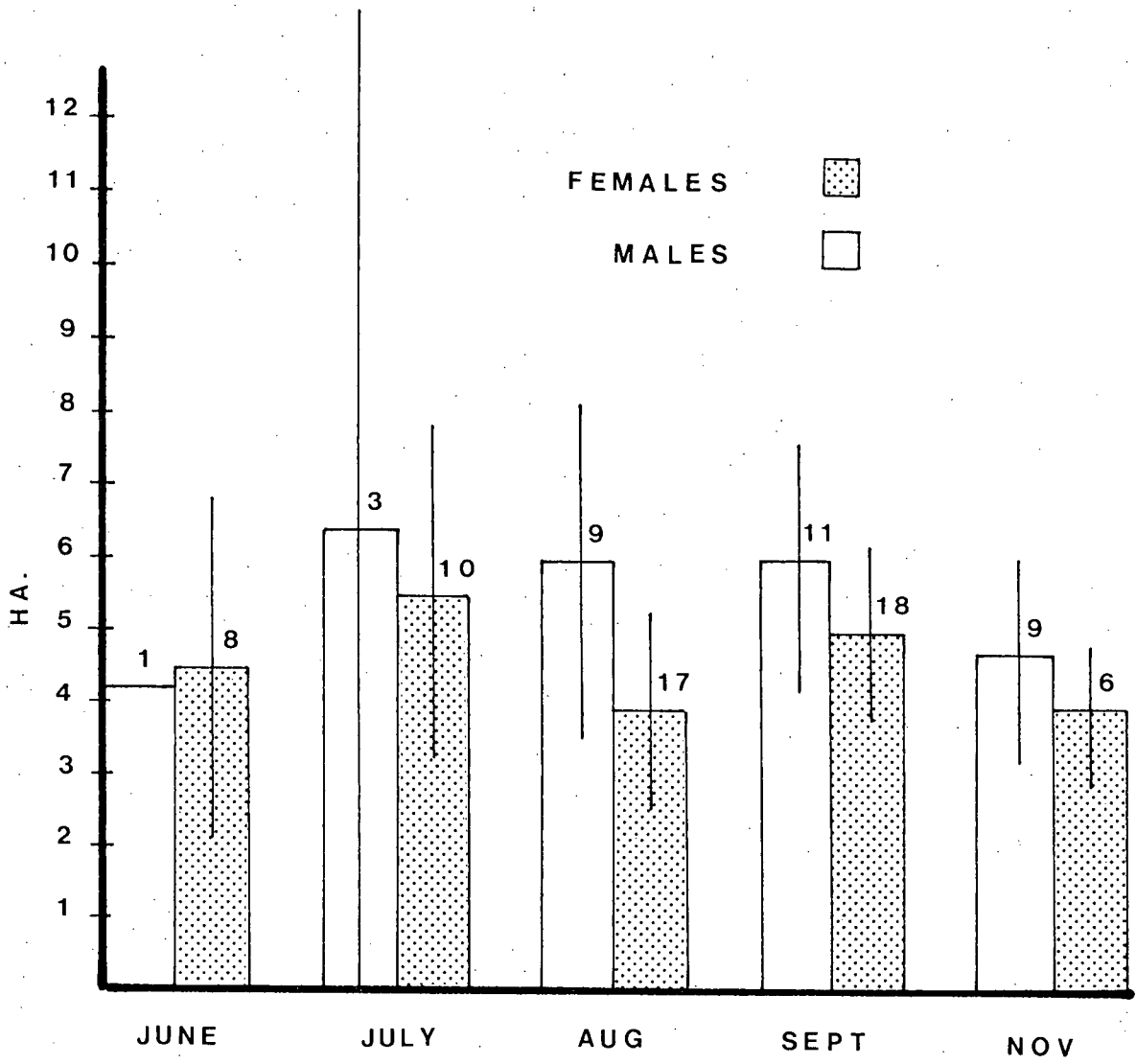
Figure 13.
    1979 mean monthly home range sizes of radio-tagged hares.
    Females had significantly smaller (t-test, P < .01) home
    ranges than males in all cases except on Telemetry in May
    and July. Narrow bars represent 95% confidence intervals.
    Sample sizes are paced above each column.
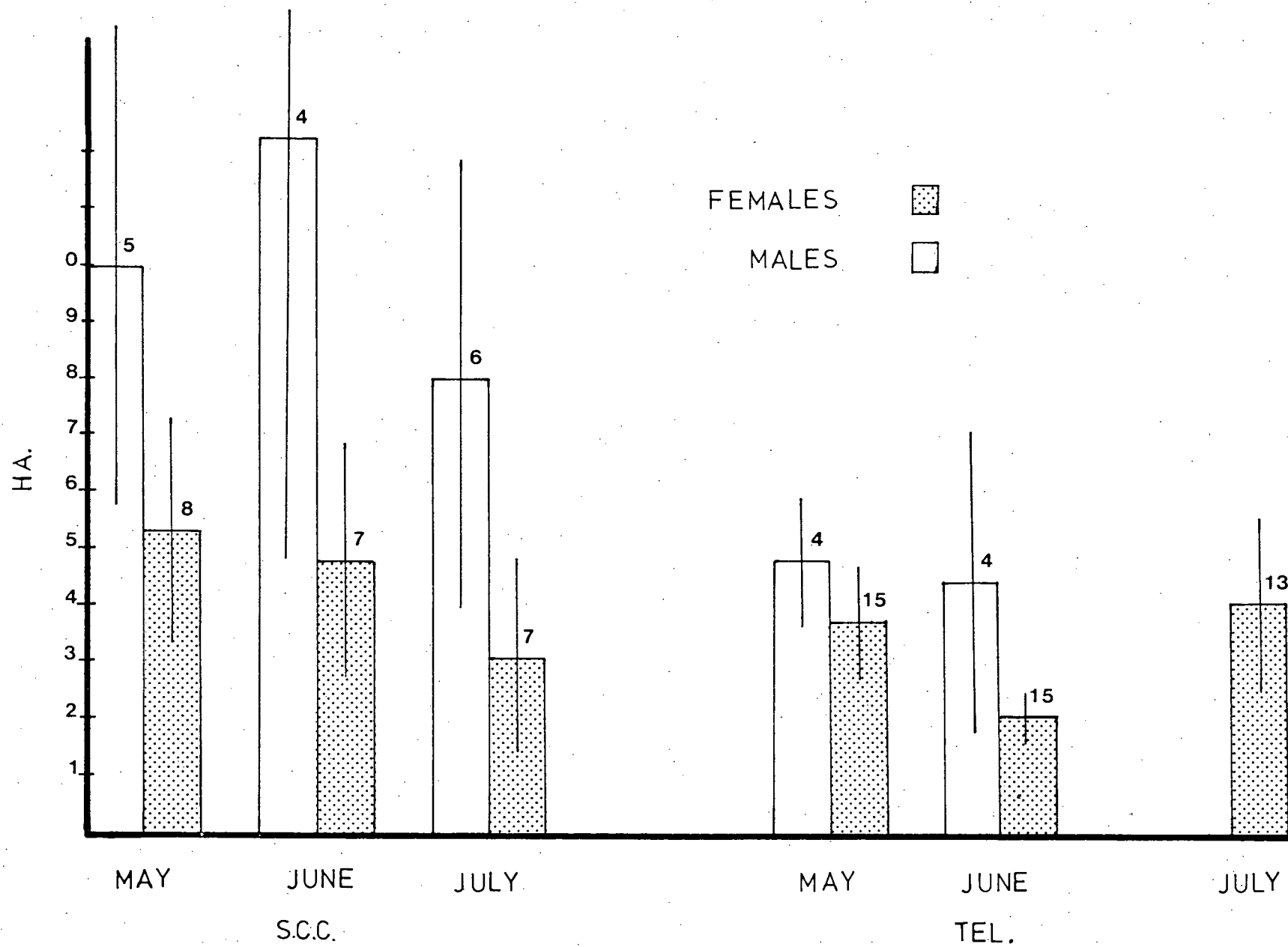
were equal. This was done to avoid biases due to sample sizes as pointed out by Jennrich and Turner (1969). Results are shown in Fig. 14. Home ranges were very small during the first two sampling periods of 1978. This is probably due to the fact that locations during this time were determined by using a handheld antenna to get very near the animal. As a result animals were located during daylight hours only, which may have resulted in an underestimation of home range size. After these two initial periods average home range size was 35% lower during birth vs. interbirth periods. The only significant diference between birth and interbirth periods was that of litter 1 on Telemetry in 1979 (P<.01) when birth ranges were 40% smaller than those of interbirth periods.

5.2-2. Percentage Overlap

Home range overlap of males and females during the breeding season was analyzed to determine how individuals arranged themselves spatially at this time. Fig. 15 shows that female 90% home ranges overlapped extensively. Actual percentages are shown in Fig. 16. The breeding season was again broken down into periods centered around and between the birth of litters. Average overlap was never less than 30% and was 20% lower during birth (40%) vs. interbirth (60%) periods.

Female home range overlap was further analyzed to determine if intensively used areas of an individual's range were overlapped by others. 50% home ranges were taken as representing these more intensively used areas as suggested by Michener

Figure 14.
    Mean home range sizes of females showing smaller range
    sizes during birth versus interbirth periods. Grids have
    been combined except during the birth of litter 1 in 1979
    when home ranges in the two areas were significantly
    different. Narrow bars represent 95% confidence intervals.
    Sample sizes are placed above each column.
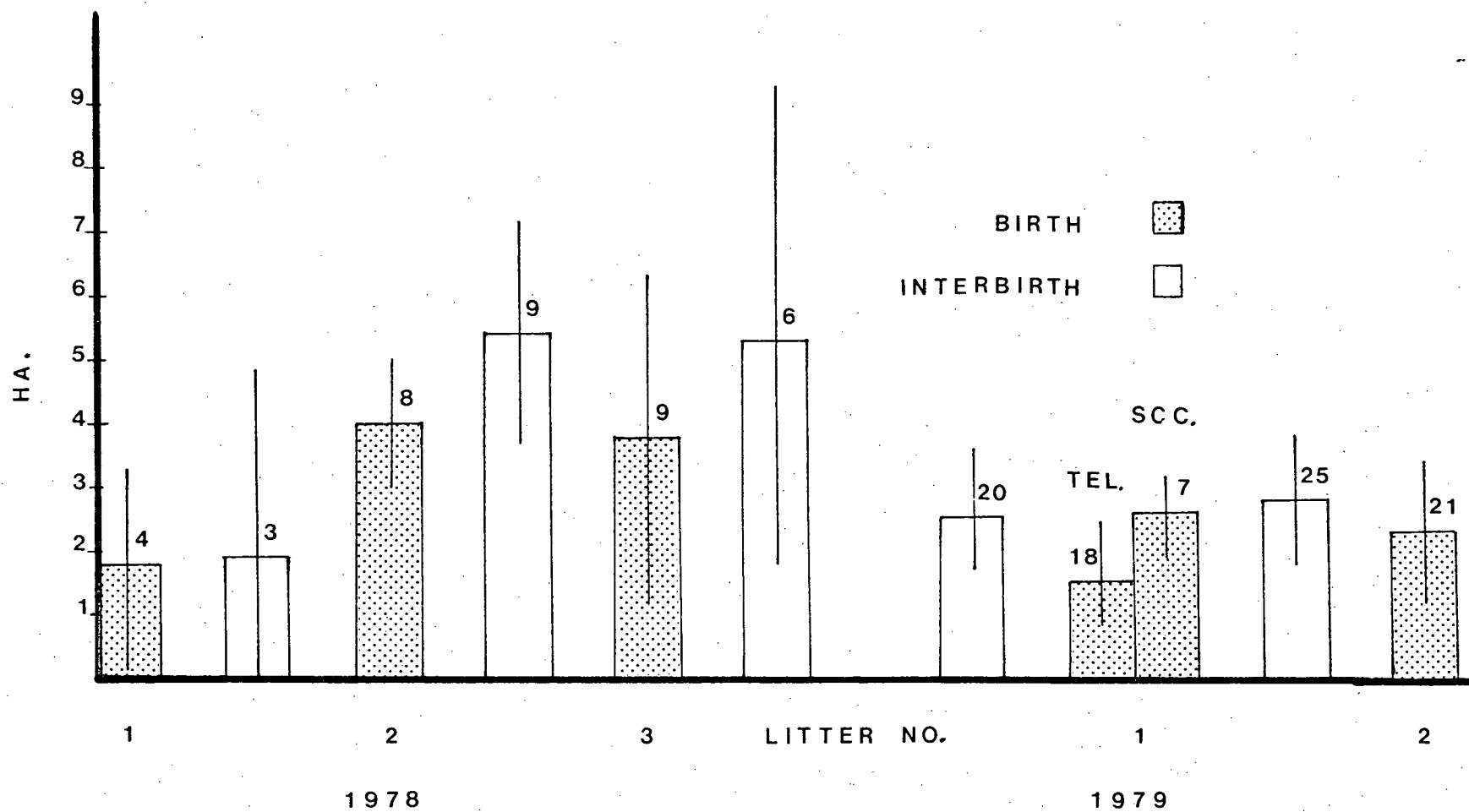
Figure 15.
    Female 90% home ranges on S.C.C. showing extensive overlap
    during the breeding season.

MAY 15 - 30 1979

N
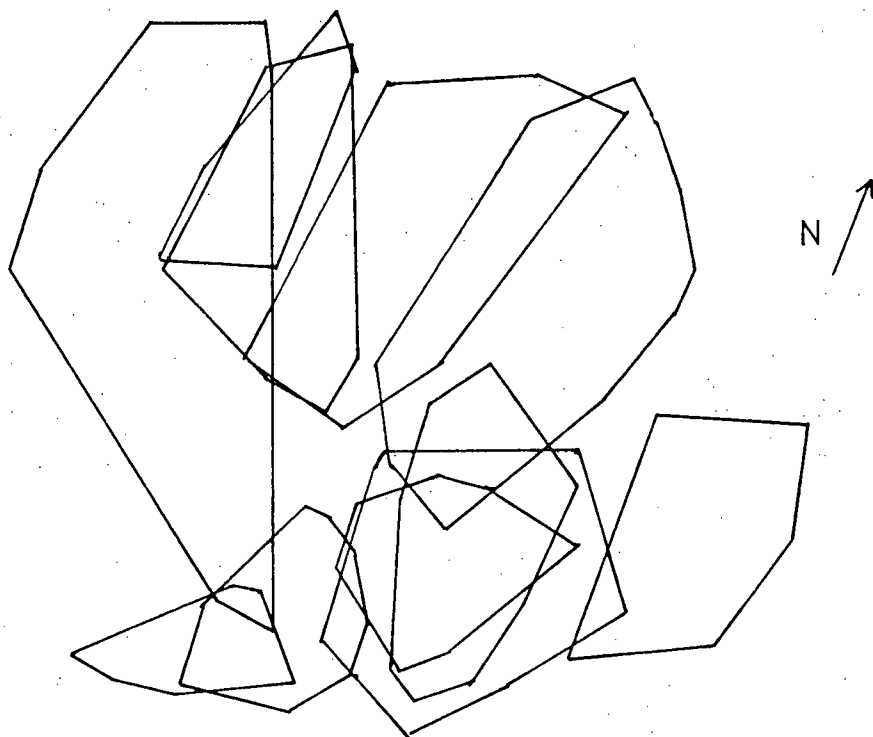
150 m

Figure 16.
      % overlap of female home ranges during birth vs.
      interbirth periods. Home ranges were determined over two
      week intervals in 1978 and weekly intervals in 1979. All
      percentages have been transformed by arc sine square root
      function. 95% confidence intervals are shown by narrow
      bars and sample sizes are placed above each column. Notice
      the lower amount of overlap during birth periods.
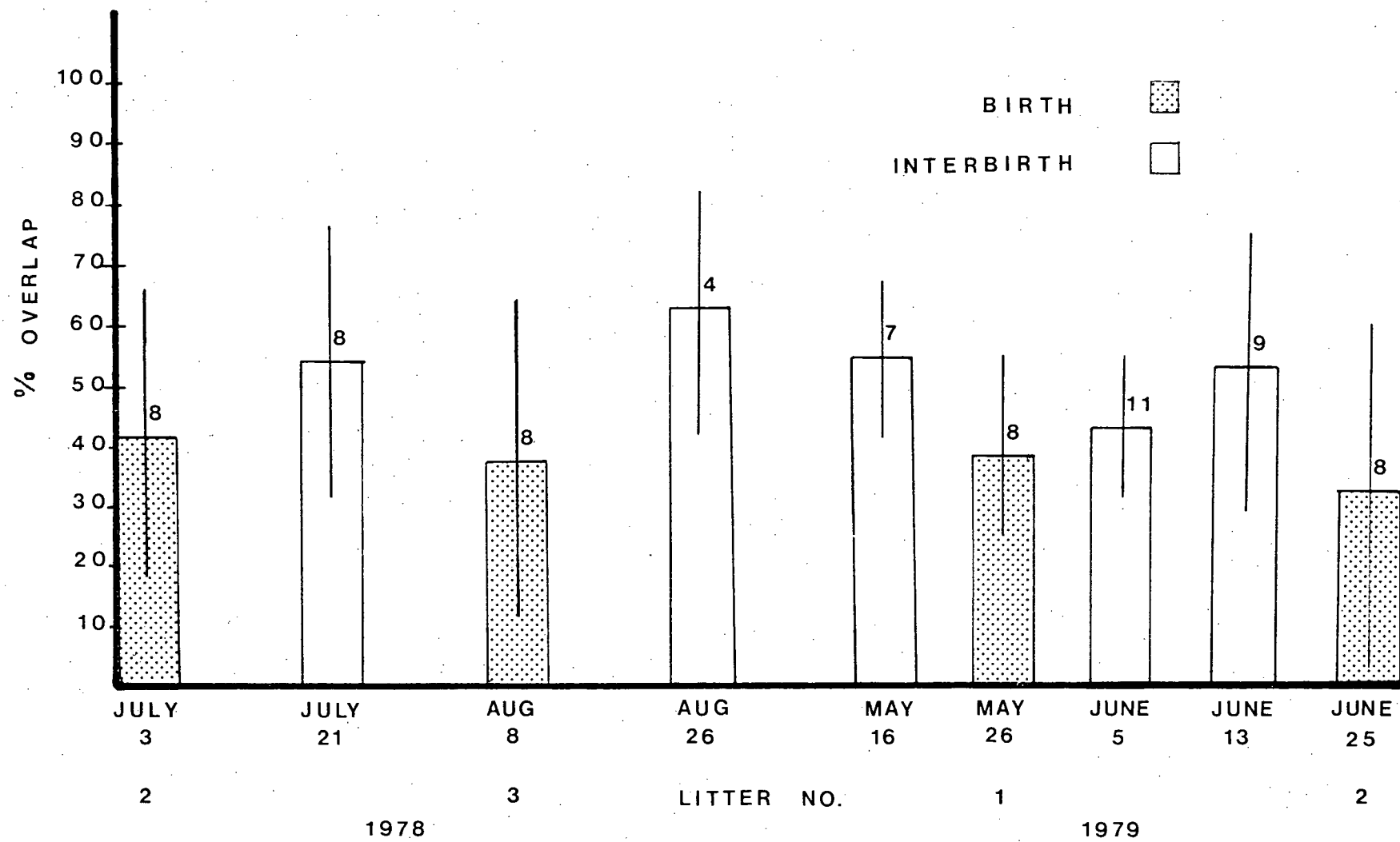
(1979). The 50% home range of an individual female was plotted on a map and the 90% ranges of all other individuals were superimposed on it. Percentage overlap was determined and found to be as high in these 50% areas as it was when 90% home ranges were considered. There was no suggestion that females avoided areas used extensively by another female.

Male 90% home ranges also overlapped extensively during the breeding season as shown in Fig. 17. As with females, mean values were never less than 35%. Fig. 18 shows that males overlapped females and did not exclude other males from females within their range. An individual male could come into contact with as many as seven females but the average was just over three.

Animals did not change their spatial arrangements outside of the breeding season. Fig. 19 shows that in November 1978, ranges continued to overlap between and within sexes, and a similar arrangement occurred in early March 1979. It seems that hares never exclude individuals of the same or opposite sex from part or all of their home range at any time of the year.

5.2-3. Dispersal

The majority of animals radio-tagged during the study occupied the same home range throughout the year. However, 14 of 116 tagged individuals did undergo dispersal movements. Dispersal was considered to be any movement in which an animal left its home range and did not return. Table 4 lists the 14 dispersers along with their age, sex, time and distance of

Figure 17.
    90% home ranges of males on S.C.C. showing high overlap
    during the breeding season.

MAY 15 - 30 1979

150 m

N
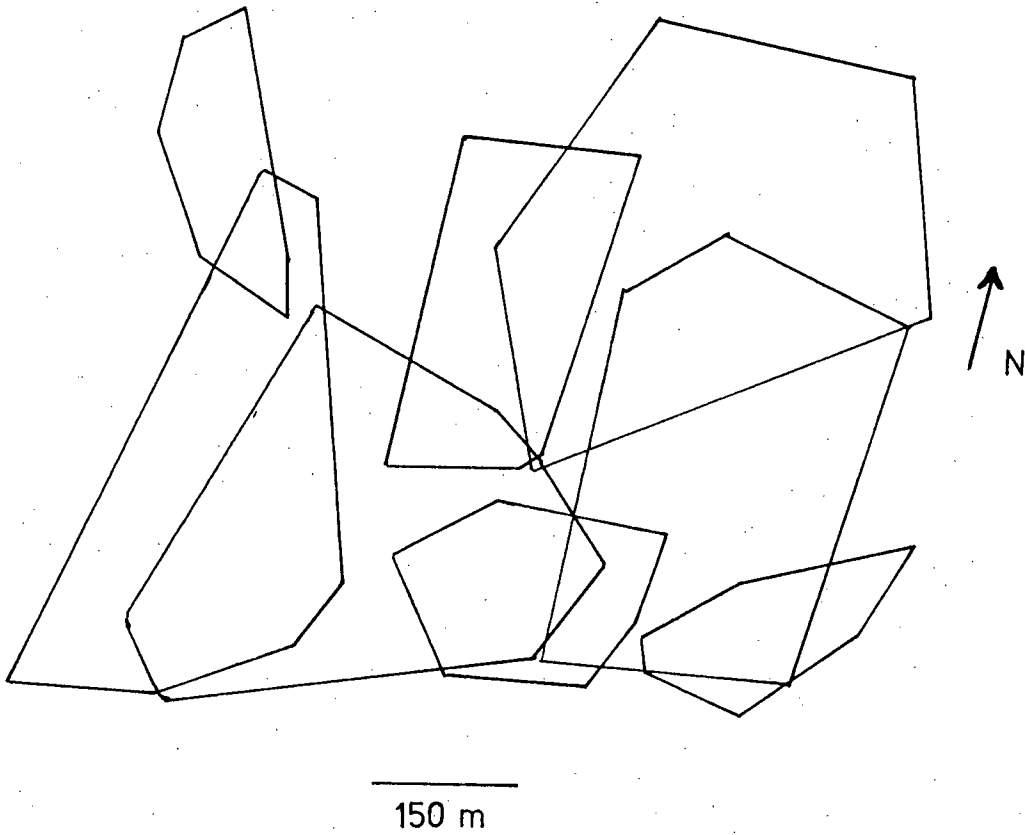
Figure 18.
    90% home ranges of 3 males (---) and 5 females (- - -) on
    S.C.C. showing high overlap between and within sexes.

MAY 15-30 1979

100 m

N
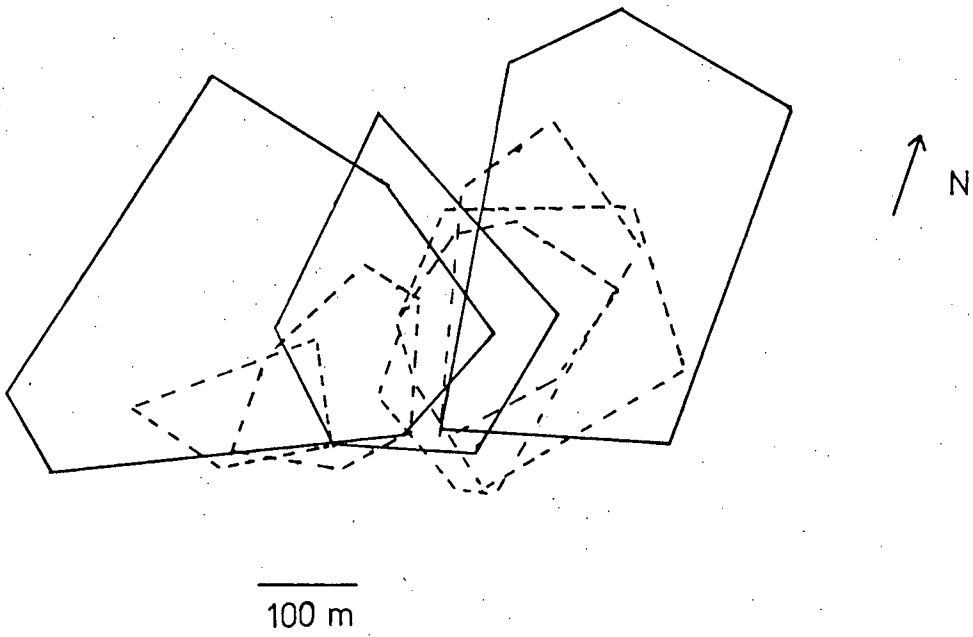
Figure 19.
    90% home ranges of males (---) and females (- - -) on the
    study areas during November 1978. Notice the overlap
    between and within sexes.

S.C.C.
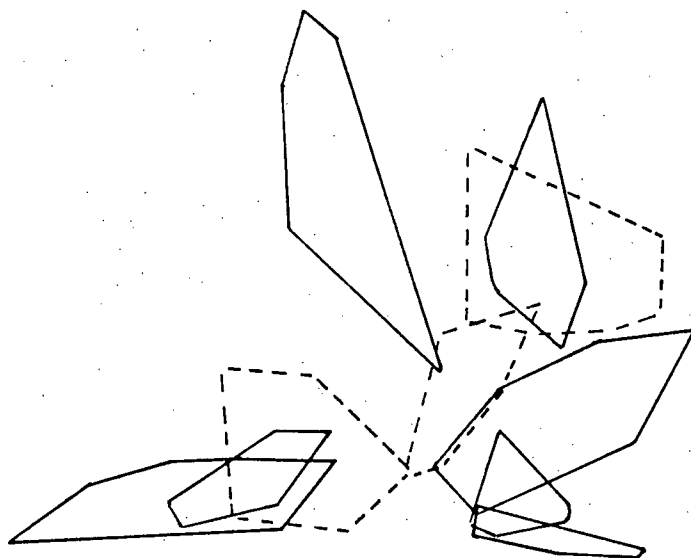
TELEMETRY
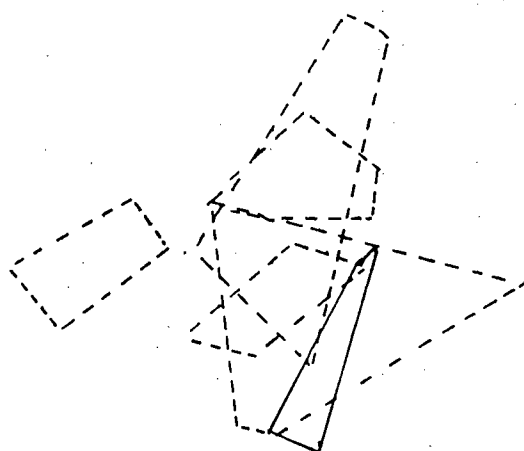
100 m

TABLE 4

Status,grid,timing of movement,distance moved,and final fate
of hares dispersing during the study.

| GRID | STATUS | | | TIME OF DISPERSAL | DIST. MOVED (M) | FATE |
	LITTER	SEX	AGE AT DISPERSAL			
SCC	1	m	juv.	July 28/78	850	mortality
SCC	1	m	juv.	July 29/78	860	dispersed
				Sept. 3/78	1524	mortality
SCC		f	ad.	Nov. 12/78	2670	mortality
SCC	2	f	juv.	Dec-Feb	460	mortality
SCC	2	f	juv.	Dec-Feb	500	mortality
SCC	2	f	juv.	Dec-Feb	460	removed
SCC		f	ad.	May 20/79	2290	unknown
Tel.	1	f	juv.	July 29/78	760	unknown
Tel.		f	ad.	July 30/78	1200	mortality
Tel.	2	m	juv.	Sept. 25/78	890	mortality
Tel.	2	m	juv.	Sept. 26/78	840	unknown
Tel.	1	f	juv.	Oct. 30/78	615	dispersed
				** April /79	615	removed
Tel.	2	f	ylng	Nov-Mar	1000	alive
Tel.		f	ad.	May 5/79	915	alive
*		f	ad.	June 20/79	1370	removed

*caught in peripheral traps near Telemetry Grid

**animal returned to its original home range

movement, and their final fate. Included in the table is a female which left its home range in late October to occupy an area 700 meters away. It remained in this location until mid-March 1979 at which time it returned to its old home range. This was the only animal which showed this migratory type of movement.

Dispersal was primarily by juveniles but did occur in all age and sex classes with the exception of adult males. This was probably due to the fact that few adult males were radio-tagged. Animals dispersed at all times throughout the study and moved a mean distance of 1045 meters. Of the 10 animals which dispersed prior to May 1979 and whose fate was known, three survived to breed in 1979. Only two animals dispersed after May 1, 1979 and both survived to breed in their new range.

5.3. Discussion

A wide variety of techniques have been used to define the home range of an animal (Stickel 1954; Jennrich and Turner 1969). Each has its favorable and unfavorable points. I chose to use the convex polygon method because of its simplicity and historical prominence. Its major shortcoming is that as sample size increases so does home range size. To see how this bias affected estimates in this study I plotted home range size against the number of radio-locations used. Home range size increased with additional locations until a total of 20 were reached, at which time an increase in locations caused little or no increase in range size. As a result I tried to use at least

20 points for all home range estimates. As a futher precaution against sample size bias, all comparisons of home range size were made with values estimated from equal numbers of locations.

The relative size and spatial arrangement of members of a population will depend to some extent on the social organization of that group. Knowing the social organization of a population then, should allow one to predict the type of spatial organization of home ranges of its members. In turn, knowing this arrangement for a species whose social organization is unknown should allow one to make inferences about its social system. I will now try to do this for snowshoe hares.

If the breeding season is considered first, there are two basic types of social organization shown by mammals (Crook 1977; Jewell 1976). These are based on the mating systems involved and can be defined as monogamy and polygyny. In monogamous systems males mate with a single female and usually participate in the rearing of young. One would expect home range sizes to be similar between sexes and the ranges of pairs to overlap extensively. Neither of these occurred in this study. Male home ranges were larger than females' which agrees with the findings of Bider (1961). Also, there was no association of one male with one female. Severaid (1942) found that male hares mated with more than one female. It seems unlikely therefore, that hares have a monogamous mating system.

Polygynous mating systems are those in which males mate with more than one female. The way in which they obtain access to additional females determines how their home ranges are spatially arranged. The various methods can be grouped in the

following manner:

(1) <u>home range abandonment</u> - Smith (1968) found that male red squirrels abandon their regular home ranges during the breeding season to roam over relatively large areas in search of receptive females. In this system male ranges would be extremely large during the breeding season and probably bear no relationship to their initial position prior to breeding.

(2) <u>territorial polygyny</u> - This mating system is characterized by breeding males obtaining exclusive rights to females either directly by defending females against other males or indirectly by defending a resource required by females (Emlen and Oring 1977). In either case males would show larger home ranges than females and would overlap more than one female home range. More importantly, male-male home range overlap would be minimal as a result of males actively preventing other male access to females in their home ranges. A variation of this type of territorial system is one in which males defend very small territories through which females move in search of mates. This is found in a number of ungulate species (Jarman 1974). Home ranges of males in this situation would be smaller than those of females.

(3) <u>dominance heirarchy polygyny</u> - In this system males gain access to females by being behaviorally dominant to other males in the area. A dominant male would then have access to any females within its home range. Home ranges of males would again be larger than those of females. The

major difference from a territorial polygynous system would be that male home ranges would overlap both female and male ranges. Males would not exhibit exclusive areas.

(4) promiscuous polygyny - This system would possess the same spatial organization of home ranges as the previous system. In this case however, any male overlapping a female's home range would have an equal chance of mating with that female. There would be no differential access according to aggressive interactions between males.

The spatial arrangement of snowshoe hare home ranges is most similar to that predicted by the dominance hierarchy or promiscuous polygyny system. Males show larger home ranges than females and there is high male-male overlap. The fact that males did not maintain exclusive areas rules out the possibility of a territorial polygynous system existing. As well, the fact that males remain in their pre-breeding home ranges throughout the breeding season makes the home range abandonment system unlikely. It is impossible to differentiate between dominance hierarchy and promiscuous polygyny systems on the basis of home range spatial arrangements alone. Doing so would require behavioral or genetic data. Observations in the wild or in large enclosures would suggest whether certain males were dominant to others. Genetic markers could be used to determine how many females a male mates with. In a promiscuous system this should be relatively even among males while in a dominance hierarchy some males should do the majority of mating.

The various spatial systems discussed so far have been related to how the male attempts to obtain mates. Unlike males,

female home range location should be dependent on the welfare of the offspring as well as mate selection. Females should arrange themselves then, in a manner that allows the requirements or rearing young to be met. One of these might be a suitable parturition site. Bider (1961) felt that female snowshoe hares were territorial just prior to parturition and Rongstad and Tester (1971) found that females contracted their home range at this time. If females were territorial during this period their home ranges should show little or no overlap. This was not the case. Percentage overlap did decrease during periods of parturition but still remained greater than 35%. The decrease was most likely due to the fact that home range size decreased and consequently, the amount of overlap would be expected to decrease by chance alone. The decrease in home range size by females may have been due to decreased activity at this time and not an attempt to avoid other individuals. However, Michener (1979) found that female Richardson's ground squirrels did not defend territories but contracted there range during pregnancy and were much more likely to be dominant to other animals in their core area. The degree and outcome of aggressive interactions was dependent on location then, even though exclusive areas were not maintained. Hares might behave in a similar manner.

There is a possibility that females may maintain exclusive areas during parturition but do so for only a short period of time. The weekly and biweekly periods of analysis used in this study may have been too long to detect this type of short term spacing. Determining whether or not this was true would require

intense radio monitoring during the time each female was to give birth. Enough locations could then be obtained to produce accurate estimates of home range over shorter time periods.

The spatial arrangement of home ranges remained unchanged throughout the breeding season. There was no indication that either sex attempted to defend resources by maintaining exclusive home ranges. This lack of territorial spacing suggests that hares gain preferential access to resources in some other manner. One possibility is the formation of a dominance heirarchy as observed by Lindlof (1978) in European hares. Another explanation could be that resources are not in short supply during periods of increasing hare numbers such as in this study. As a result, aggressive spacing would not necessarily be apparent. Hares may in fact, shift their spatial arrangement as densities increase but only further monitoring during peak and decline years would indicate whether this is so.

Dispersal was primarily by juveniles and occurred throughout the study. There did not appear to be a specific time in which the majority of animals dispersed. This was similar to the findings of Windberg and Keith (1976) and suggests that factors triggering dispersal do not act or change at a specific time. Possible factors causing juvenile dispersal will be discussed in a later section.

Lidicker (1975) pointed out that two types of dispersal can occur in natural populations. The first, termed saturation dispersal, occurs when populations are at carrying capacity, and emigrants of this type are usually subordinate animals in poor physical condition with little chance of surviving. The second

type, pre-saturation dispersal, occurs when populations are below carrying capacity, usually during increase, and include individuals such as pregnant females which have high reproductive potential. The problem with this method of describing dispersal types is in deciding whether or not the population is at carrying capacity. I have no data concerning this question. However, hare populations on S.C.C. and Telemetry were increasing, and a number of pregnant females did show dispersal movements suggesting that some pre-saturation dispersal was occurring. It seems that the key to deciding between these two types of dispersal is knowing whether dispersers were forced to leave their home area or left on their own accord. Data on the social status of dispersers and non-dispersers would help to answer this question.

To summarize, high male and female home range overlap during the breeding season suggests that snowshoe hares have a promiscuous or dominance hierarchy mating system. There was no evidence to suggest that females defend parturition sites as suggested by Bider (1961). Hares did not attempt to maintain exclusive areas during the non-breeding season, suggesting that resources were divided among individuals by some other means.

6. FEMALE SPACING BEHAVIOR

Keith (1974) stated that lagomorphs, including snowshoe hares, are "... incapable of self-regulation below densities determined by available food supplies." Much of the work by Keith and his associates has been aimed at elucidating the relationship between changes in hare numbers and food supply (Pease et al. 1979; Keith and Windberg 1978). No work has been directed toward examining the importance of behavior on these changes in numbers. Chitty (1960) postulated that "... all species are capable of limiting their own population densities without either destroying the food resources to which they are adapted, or depending on enemies or climatic accidents to prevent them from doing so." He later pointed out that this limitation was brought about by aggressive spacing behavior passed from one generation to the next by genetic mechanisms (Chitty 1967). Further work by others has shown that both food and behavior can be linked in complicated ways that limit population numbers (Miller and Watson 1978; Watson and Miller 1971; Gibb et al. 1978). It seems important then, to examine snowshoe hare behavior, particularly aggressive spacing behavior, and its relation to population dynamics.

When the behavior of animals cannot be observed first hand, indirect methods must be employed to obtain some understanding of this factor. A number of studies have shown that removal of various types of individuals is one such indirect method that has proven particularly useful (Jenkins et al. 1963; Redfield et al. 1976). I used this approach to answer the question: How

are the movements of individual female hares influenced by the presence of other females? In other words does use of an area by one hare affect use of that area by another? I chose females because there is some suggestion that this sex is particularly sensitive to other individuals just prior to parturition (Grange 1932). This may be similar to territorial nest defence in female voles as suggested by Krebs (1978a). As hare numbers increase, spacing at this time may become more and more important.

To examine the influence of hares on each other's movements I removed a group of females from the Telemetry area and monitored subsequent movements of the remaining individuals. The basic design of the experiment was to:

(1) radio-tag a number of adjacent females and determine their home ranges.

(2) create a vacant area surrounded by radio-tagged individuals by removing the innermost members of the group.

(3) monitor subsequent movements of the remaining females by telemetry and compare these movements to females on a control area.

One would predict no difference between the types of movement shown by control and experimental females after the removal if females had little or no influence on each other's movements. Conversely, differences would suggest some effect. More specifically, if females were prevented from using areas occupied by other females one would predict that:

1. females surrounding the removal area would increase their use of that area by shifting the boundaries of their

home range.

2. females may immigrate from somewhere beyond the ring of radio-tagged females and come to occupy the removal area. If females influence the movements of other females within their home ranges and do so in a manner that causes minimal interaction one would predict that females surrounding the removal area should increase use of the portion of their home range nearest the removal.

6.1. Methods

In March 1979 all females on S.C.C. and Telemetry were radio-tagged. To increase sample size on Telemetry I began to trap the area surrounding the grid on a weekly basis. Traps were initially placed on all sides of the grid at distances up to 350 meters away. However, after a number of days it became clear that no animals were present on the western edge of the grid. Consequently, traps in this area were moved to places of greater hare activity. Any females caught in peripheral traps or on the actual grids were radio-tagged and monitored. Each was located up to four times daily; prior to 1000 h, 1100-1700 h, 1800-2100 h, and after 2200 h. In most cases animals were active during three of these four periods. Every week traps were set on S.C.C. and Telemetry for two days. During this time individuals were radio located only once each afternoon. This system produced roughly 20 locations per animal between trapping sessions and was followed throughout the experiment.

Four females were removed from Telemetry on May 12, 1979.

Movements of the remaining animals were compared to females on S.C.C. which served as an experimental control. Prior to the removal, the home ranges of 19 females on the Telemetry area and 11 females on S.C.C. were known from up to 18 days of radio locating and as many as 35 actual locations per animal. The relative locations of the four individuals that were removed can be seen in Fig. 20. These specific animals were chosen for the following reasons. Firstly, they were located on the actual grid, the area in which I was most confident that all females had been captured and radio-tagged. As well, trapping intensity was greatest in this area and thus afforded the best chances of catching any new animals immigrating. Secondly, this area had supported four adult breeding females in 1978. It seemed likely then, that it was capable of doing so in 1979.

The animals were removed 10 days before the first litters were born. Remaining individuals were monitored until June 20, at which time the experiment was repeated. Results of the first removal will be given before details of the second are outlined.

6.2. Results

6.2-1. Removal Number One

6.2-1-1. Use of the Removal Area

To test if females increased their use of the removal area I compared the proportion of radio locations found in the vacated area before the removal with that afterwards. Table 5

87

Figure 20.
    Relative locations of female home ranges on Telemetry
    before the removal. The dark polygon represents the area
    occupied by the four females (R1, R2, R3, R4) which were
    removed.
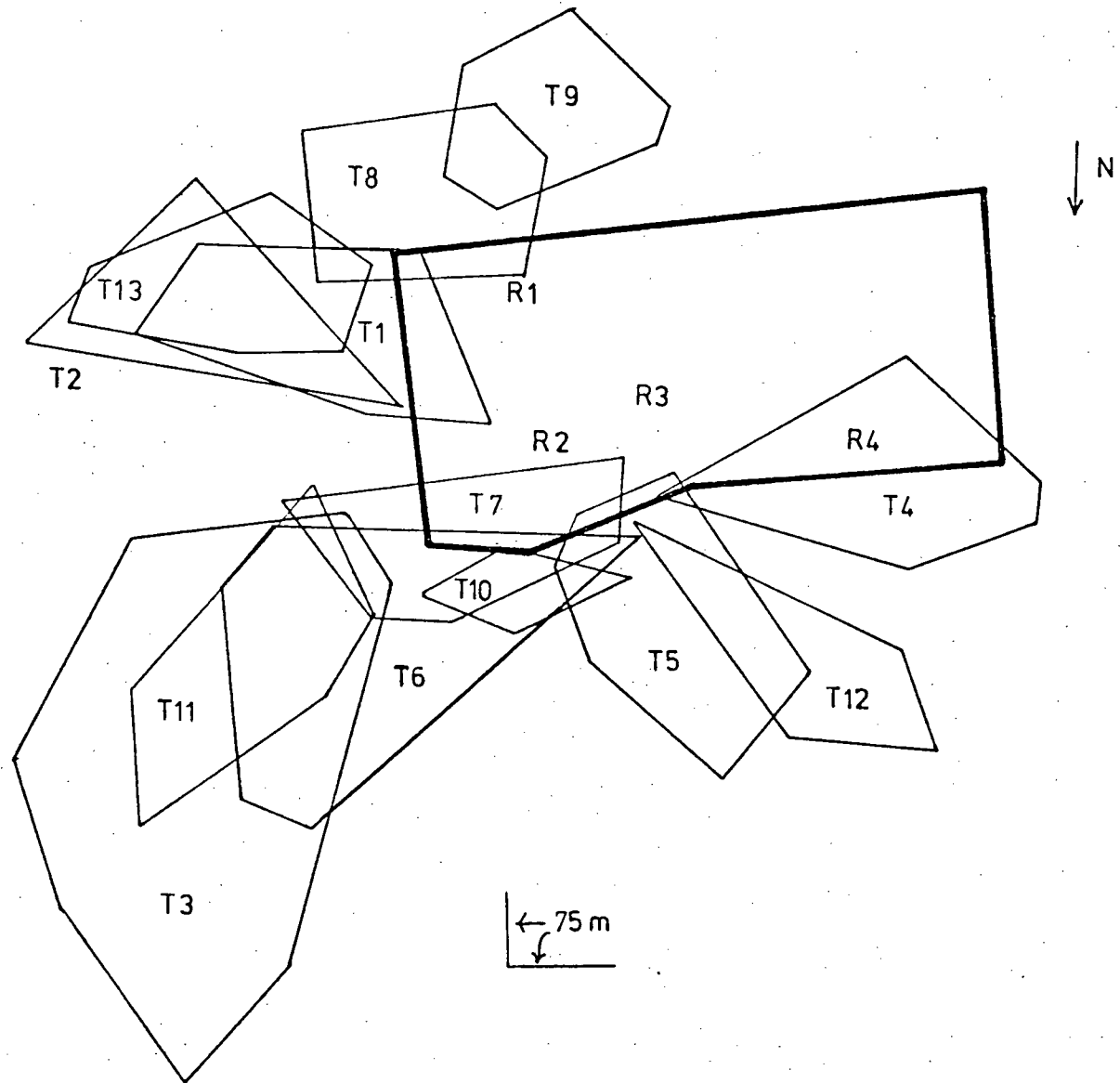
TABLE 5

Changes in the proportion of locations found in the removal area following the first removal.

HARE NO.	MAY 12-21	MAY 22-31	JUNE 1-8	JUNE 9-20
T1	+0.45	-0.30	-0.01	+0.05
T2	+0.10	+0.03	-0.23	-0.14
T3	-0.02	-0.07	-0.07	-0.07
T4		PREDATOR KILL		
T5	-0.10	-0.04	-0.10	-0.10
T6	+0.15	+0.06	0.0	-0.02
T7	+0.37	+0.13	+0.23	+0.27
T8	+0.09	+0.09	-0.15	-0.01
T9	+0.08	0.0	-0.06	-0.06
T10	-0.06	-0.06	-0.06	-0.06
T11	1	1	+0.29	+0.50
T12	0.0	0.0	0.0	0.0
T13	0.0	0.0	0.0	0.0
*T14	0.0	0.06	0.09	0.04
*T15	0.66	0.60	0.39	0.86
*T16	0.0	0.11	0.05	0.13
no. animals showing increase	6/11	4/11	2/12	3/12

*Proportions for these animals represent the actual proportion of locations found in the removal area. No locations were obtained before the removal.

1 - Lost Radio Contact

shows the changes occurring in four successive periods following the removal. If all females are considered together, use of the vacated area was never significantly greater after the removal (Wilcoxon's signed-ranks test, P>.05). However, three individuals (Hares T7,T11, and T15) did show substantial increases in their use of the area. A fourth, hare T1, did so for one week.

Hare T15 spent the majority of its time after the removal in the vacated area. Unfortunately, its home range was not known before the manipulation. However, it was never captured in the removal area prior to the removal. All other radio-tagged females that had greater than 25% of their radio-locations in the vacated area were captured at least once prior to the removal. This would indicate that hare T15 spent little time in this zone before the removal.

Hare T11 was found to have increased its use of the vacated area after the removal. It may have done so sooner but its home range could not be determined immediately after the removal because of a malfunctioning radio.

Fig. 21 shows that no noticable shift in home ranges occurred after the removal. Any increase in use was restricted to the outer edges of the vacated area while the bulk remained unused. No animal shifted its home range to occupy the removal area exclusively.

To summarize, although a few animals showed major increases in use of the area vacated by the removal, the overall change was not significant and the majority of the removal area remained unoccupied.

Figure 21.
     Relative locations of female home ranges before and after
     the first removal. Dotted lines indicate home ranges of
     animals newly tagged after the removal. Notice that the
     removal area remained unoccupied.

PRE-REMOVAL

T9

T8

T13

T1

R1

N

T2

R3

R2

R4

T4

T7

T10

T6

T5

T12

T11

T3

←|75 m

POST-REMOVAL

T9   T18

T8

T17

T13

N

T14   T2   T1

T15

T19

T3

T7

T11

T5

T16

T12

T6

T10

←|75m
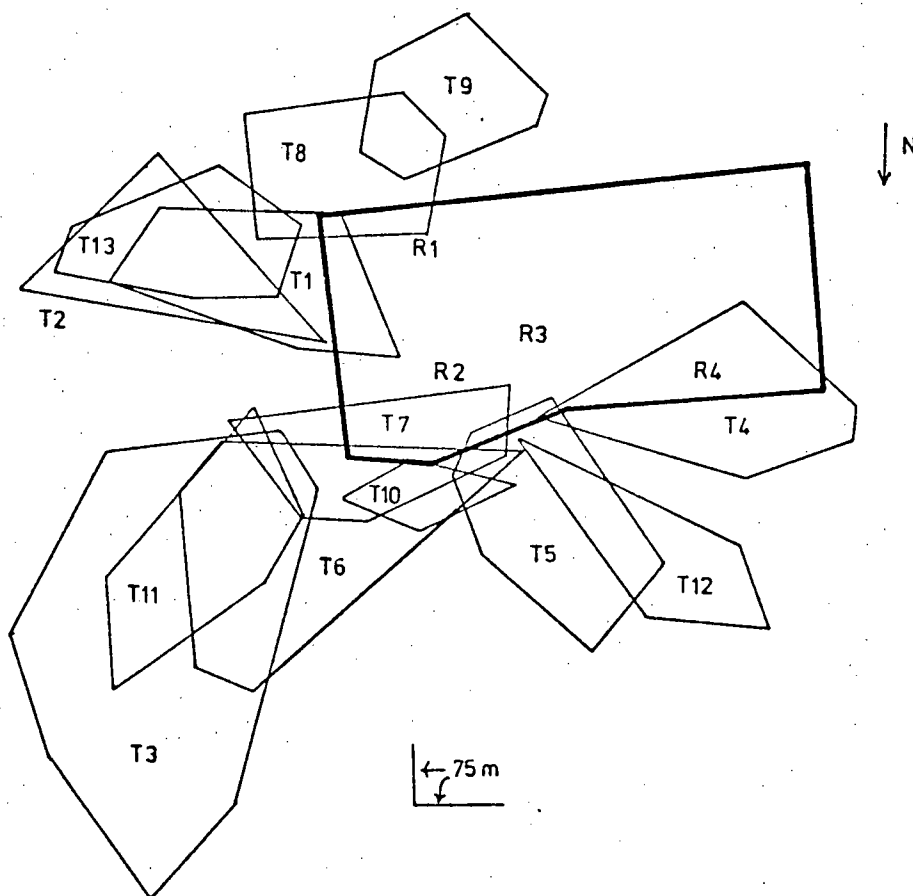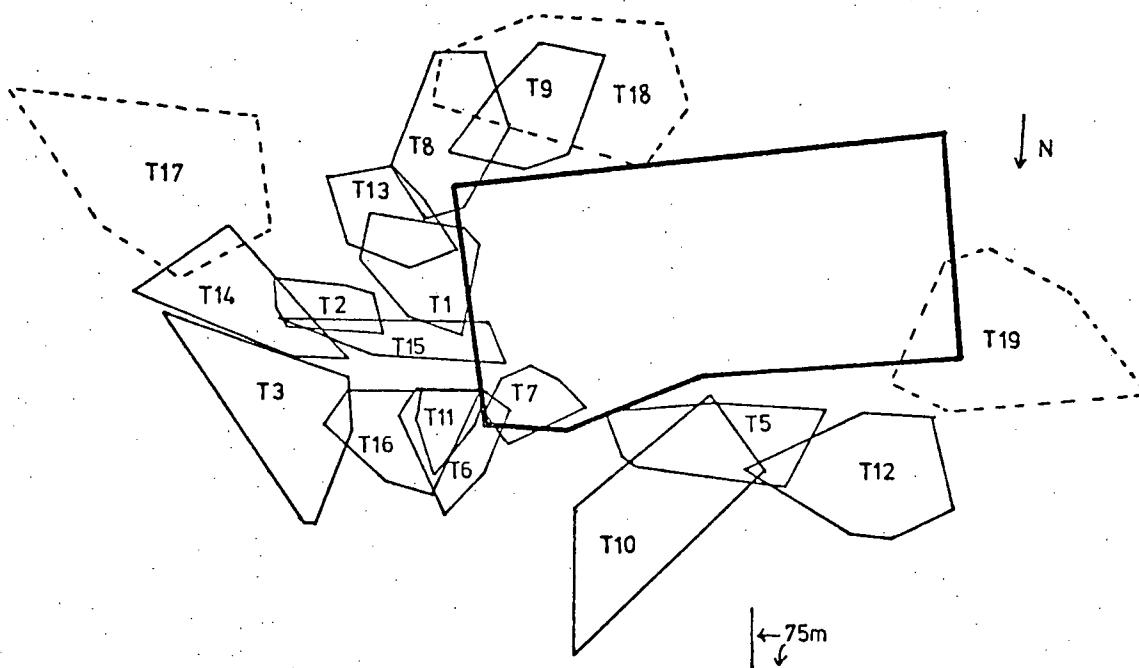
6.2-1-2. Home Range Use

Females did not shift their home ranges after the removal but they may have responded by altering movements within their home range. If females avoid each other one would expect them to use their home ranges in a manner that minimized interaction. If so and some individuals were removed, females would be expected to increase their use of the portion of their home range nearest the removal area.

To test if this occurred I performed the following analysis. The 90% pre-removal home ranges of all females surrounding the removal area were determined. I then located the centre of the removal area and drew a line from it through the arithmetic centre of each female's home range. Perpendicular to each of these lines another line was drawn through the median point of each home range. This bisector served to divide the radio locations of each female's home range into halves, leaving 50% of the locations on the side of the bisector nearest the removal area. Finally, these bisectors were superimposed on each appropriate female's home range during four consecutive nine day time periods following the removal. The proportion of radio-locations on the removal side of the lines were determined in each case.

Table 6 shows the changes in the proportion of radio locations found on the removal side of the bisecting line. Females spent significantly more time on the removal side of their home range in all time periods except May 22-31 (Wilcoxon matched pairs test P<.005), and the response increased with

TABLE 6

Home range use by Telemetry females following the first
removal. Values represent the proportion of locations for
each animal in the half of its home range nearest the
removal area. Pre-removal values were equal to 0.50.

HARE NO.	MAY 12-21*	MAY 22-31(NS)	JUNE 1-8**	JUNE 9-20**
T1	0.92	0.05	0.43	0.42
T2	0.63	0.55	0.64	0.81
T3	1.00	0.87	1.00	1.00
T5	0.60	0.84	0.88	0.78
T6	0.89	1.00	1.00	1.00
T7	0.76	0.25	0.78	0.88
T8	0.83	0.81	0.69	0.95
T9	0.50	0.67	0.82	0.89
T10	0.14	0.74	0.78	1
T11	1	1	1.00	1.00
T12	0.50	0.67	0.69	0.60
T13	0.81	0.42	1.00	0.83
no. animals showing increase	8/11	8/11	11/12	10/11

NS - not significant
* P < .025
** P < .005
1 - lost radio contact

time. One week after the removal, animals were spending an average of 20% more time on the removal side of their home range and 8 of 11 animals showed positive increases. By June 1-8 this had increased to 30% and 11 of 12 animals.

To test if similar directional changes in home range use occurred for S.C.C. females I performed the same analysis on these individuals. The same relative grid location was used as a midpoint and lines were drawn to the centres of each female's home range. Table 7 shows the changes in home range use after the removal on Telemetry. Use was never significantly different from the pre-removal period (Wilcoxon's matched pairs test, P>.05). It should be noted however, that animals on S.C.C. did show large shifts in use of their home range, but never in any consistent direction.

To summarize, females did not respond to the manipulation by increasing their use of the vacated area. However, they did spend a significantly greater amount of time on the half of their range nearest the removal area. S.C.C. females did not show similar changes.

6.2-1-3. Number of Immigrants

Another possible response by females to the removal might be long range immigration. In other words, females other than those immediately surrounding the removal area might settle in the vacated space. I tested this by measuring the number of new adult females being caught on S.C.C. and Telemetry after the removal. The number of immigrants were similar on both grids:

TABLE 7

Home range use by S.C.C. females after the first removal.
Values represent the proportion of locations for each animal
in the half of its home range nearest the removal area.
Pre-removal values were equal to 0.50.

HARE NO.	MAY 12-21(NS)	MAY 22-31(NS)	JUNE 1-8(NS)	JUNE 9-20(NS)
S1	[1]	0.11	0.00	[1]
S2	0.93	1.00	0.94	0.84
S3	0.08	0.00	0.00	0.00
S4	1.00	1.00	0.95	0.55
S5	0.53	0.89	0.00	0.00
S6	0.25	0.50	0.00	0.07
S7	0.21	0.17	0.23	0.00
no. animals showing increase	3/6	3/7	2/7	2/6

NS - not significant   P > .05
[1] - lost radio contact

four females and four males on Telemetry and three females and two males on S.C.C. This suggests that the removal area had no influence on the number of animals immigrating. Fig. 21 shows that the new animals caught on Telemetry did not occupy the centre of the removal area but existed along its edges. It is possible that these animals were not immigrants but rather residents occupying the edge of the grid. Because they spent little time on the grid, they avoided being trapped previously.

6.2-2. Results of the Second Removal

On June 20, 1979, six more females were removed from the Telemetry area. As shown in Fig. 22, the removal of these animals served to enlarge the area vacated by removal one. The remaining animals were followed until Aug. 1 in a fashion similar to the first experiment. The only differences were that slightly fewer locations were taken each week and traps were set bi-weekly rather than weekly. Pre-removal home ranges of the remaining individuals were determined from radio locations taken during the 20 days prior to the second removal.

Table 8 shows the changes in the proportion of time spent on the removal area following the manipulation. Changes were not significantly different in any of the periods following the removal (Wilcoxon's matched pairs test $P > .05$). Hare T20 was the only animal that showed a noticeable increase in the use of the area. As well, no new adult females were captured in the removal zone following the manipulation. Fig. 23 shows that the vacated area remained unused, a result in agreement with that of

Figure 22.
    Relative locations of female home ranges on Telemetry prior
    to the second removal. The removal area created by removal
    of animals (T1,   T6,   T7, T10, T11, T15) is outlined with
    heavy lines.

PRE-REMOVAL
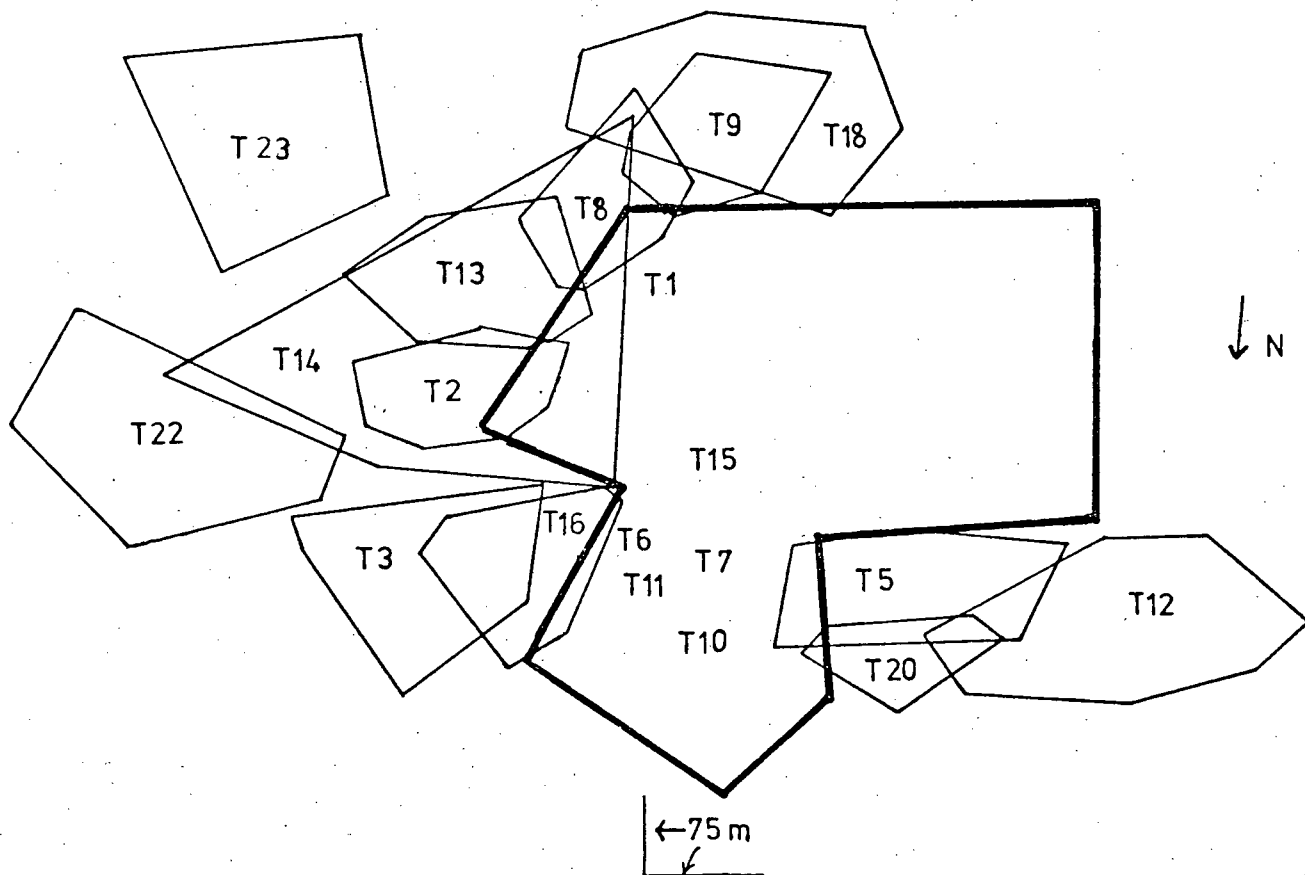
TABLE 8

Changes in the proportion of locations found in the removal
area after the second removal.

HARE NO.	JUNE 20-31	JULY 1-15	JULY 16-31
T2	+0.11	+0.04	+0.05
T3	-0.06	+0.03	-0.06
T5	+0.04	+0.33	1
T8	+0.43	-0.03	+0.06
T9	+0.04	+0.08	+0.13
T13	-0.03	+0.14	-0.03
T12	+0.05	+0.09	+0.05
T16	-0.09	1	1
T14	-0.06	0.0	-0.01
T18	+0.02	0.0	+0.03
T20	+0.04	+0.19	+0.39
*T21	0.24	0.17	0.17
*T19	0.0	0.11	0.04
no. animals showing +ve increase	7/11	7/10	6/9

*Figures for these animals represent the actual
proportion of locations found in the removal area.
No locations were obtained before the removal.

1 -lost radio contact

Figure 23.
    Relative locations of female home ranges before and after
    the second removal. Notice that the majority of the removal
    area remained unoccupied.

PRE-REMOVAL

T 23

T9

T18

T8

T13

T1

T14

T2

T22

T15

T16

T6

T7

T5

T12

T3

T11

T20

T10

↓ N.

←75 m

POST-REMOVAL

T 23

T 21

T9

T18

T13

T8

T14

T2

↓ N

T 22

T3

T16

T5

T12

T 20

←75 m
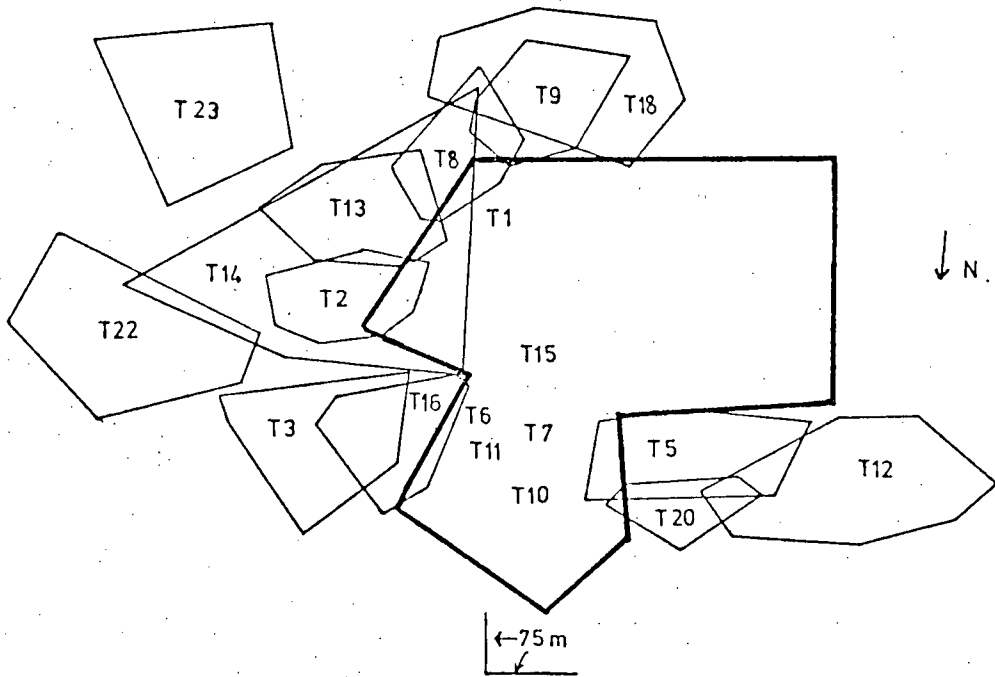
the first removal.

Table 9 shows changes in home range use after the second removal. As with the first removal, individuals showed an increase in use of the portion of their home range nearest the removal area and, in addition, the change increased with time. However, the overall difference was less pronounced in this instance and was significant only during the last two weeks of July (Wilcoxon's matched pairs test, P<.05). Table 10 shows that S.C.C. females showed no similar shifts in home range during the period after the second removal on Telemtry. Females then, shifted use of their home range in a similar fashion after each of the the two removals, although the response was less pronounced following the second removal.

6.3. Discussion

In this experiment I tried to assess the influence of spacing behavior on female movements by removing females and monitoring subsequent movements of the surrounding animals. The utility of this design is dependent on a number of assumptions.

The first of these assumptions is that the vacated areas created in each manipulation were completely free of adult females. Animals miss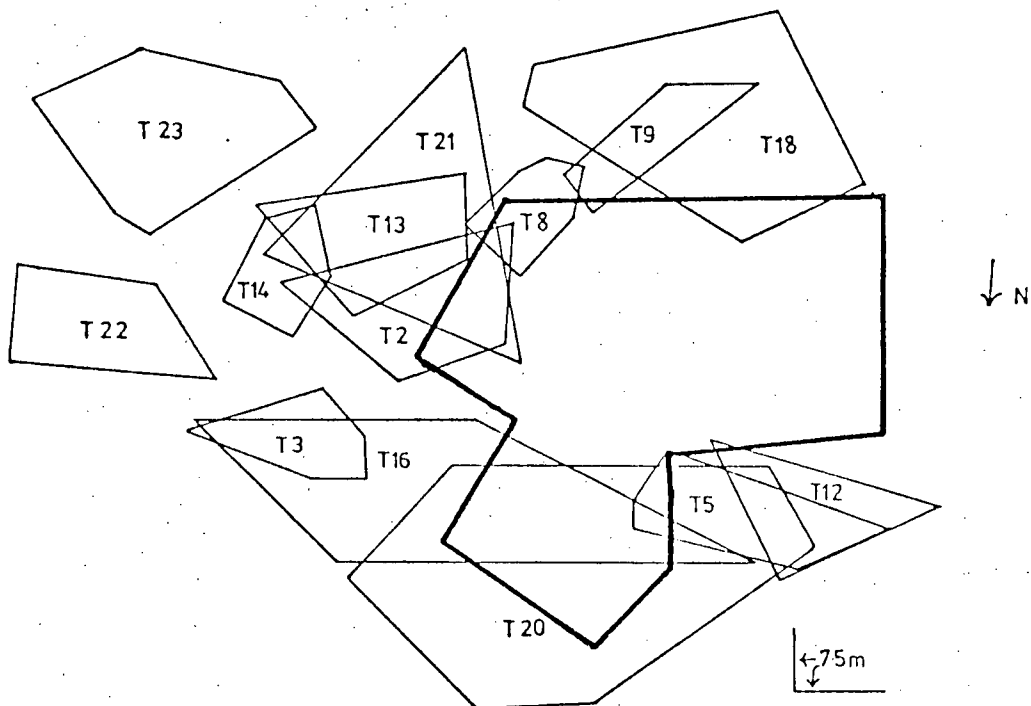ed may have prevented other females from moving into the area. To reduce the chances of this happening the removals were done in areas of highest trapping intensity. No new animals were ever captured in the middle of these areas. All were caught on the outer edge and subsequent monitoring by telemetry showed that they spent little time in the actual

TABLE 9

Home range use by Telemetry females following the second removal. Values represent the proportion of locations for each animal in the half of its home range nearest the removal area. Pre-removal values were equal to 0.50.

HARE NO.	JUNE 20-31 (NS)	JULY 1-15 (NS)	JULY 16-AUG 1*
T2	0.75	1.00	0.87
T3	0.36	0.90	1.00
T5	0.42	0.50	ı
T8	0.71	0.70	0.69
T9	0.39	0.46	0.39
T12	0.75	0.54	0.53
T13	0.08	0.50	0.43
T14	0.29	0.27	0.50
T16	0.50	ı	ı
T18	0.33	0.60	0.50
T20	0.87	0.57	0.65
T22	0.00	0.22	0.70
T23	ı	0.83	1.00
no. animals showing increase	4/12	7/12	7/11

NS — not significant P > .05
* P < .025
ı - lost radio contact

TABLE 10

Home range use by S.C.C. females following the second removal. Values represent the proportion of locations for each animal in the half of its home range nearest the removal area. Pre-removal values were equal to 0.50.

HARE NO.	JUNE 20-31(NS)	JULY 1-15(NS)	JULY 10-AUG 1(NS)
S2	0.46	0.50	0.37
S3	0.77	0.82	0.89
S4	0.78	0.93	0.38
S5	0.83	0.42	0.63
S6	0.11	0.00	0.75
S7	0.73	0.70	1
S8	0.50	1.00	1.00
S9	0.20	0.50	0.45
no. animals showing increase	4/8	4/8	4/7

NS - not significant   P > .05
1 - lost radio contact

removal area. It seems unlikely then, that trappable females at least, were missed on the removal areas. However, there is still the possibility that trap-shy animals remained. To determine if this was true a hare drive similar to that described by Keith et al. (1968) was conducted prior to the first removal. People moved through the removal area attempting to drive hares into a net. The drive was conducted twice and no animals were captured. Further support for the contention that no trap-shy hares were present in the area comes from observations made while setting and checking the trapping grids. No unradio-tagged animals were ever sighted on S.C.C. where all animals received radio-collars. Unfortunately, some males on Telemetry were not tagged and so one could not be sure that any animals without collars sighted there were females. The fact that none were sighted on S.C.C. would suggest that all animals present on the trapping grid for any length of time were captured.

The second assumption is that the removal was done at the appropriate time. The effect of spacing behavior on movement may be more important at certain times of the year. I chose the time period just prior to birth of the first litter because females appear to be most aggressive at this time. Grange (1932) observed that females would not allow males near them prior to parturition. Rongstad and Tester (1971) suggested that female snowshoe hares contract the size of their home range prior to giving birth. This may be an attempt to avoid other individuals. Haugen (1942) felt that cottontail (_Sylvilagus_ _floridanus_) females were territorial during the breeding season and Marsden and Holler (1964) obvserved some defence of nest sites. Hence

the time prior to parturition appeared appropriate for this experiment. Spacing may also be important at other times of year and further experiments will be necessary to examine these periods.

The third assumption is that the individuals removed were representative, in terms of social status, of the entire population. If for example, females were organized into a dominance hierarchy (Lindlof 1978) and only subordinate animals were removed, results could be very different from those obtained if dominant animals were removed. There is no effective way of determining if this did actually occur. However, all of the females removed were pregnant and showed no noticable differences in body weight, condition, or home range size from other females in the area. If social differences did exist, they were not indicated by these factors.

The final assumption is that telemetry locations give a reasonable estimate of home range location and use. The accuracy of the locations has already been discussed. The daily schedule of location times was designed to locate animals during periods of activity and resting, thus eliminating any biases due to differential use of home range during each behavior. Since the locating schedule was not changed during the study any unknown biases would be similar before and after the removal and consequently would not have affected the results.

Females could have responded to the removal by:

1. Increasing their use of the vacated area by shifting the boundaries of their home range.

2. Immigrating to the removal area from long distances

(beyond the group of radio-tagged females)

3. Shifting use of their home range but not changing the actual boundaries.

4. Showing no change in their movements after the removal. Females as a whole, did not increase their use of the removal area following each of the two removals. Some individuals did spend more time in the area but none showed a major shift from their old home range to the area left vacant by the removal. As well, no long distance immigrants came to occupy the removal area. Females appear unwilling to shift their home range during the breeding season, a finding similar to that of Windberg and Keith (1976). These authors reduced female density at the beginning of the breeding season in two successive years. In the first, a year of increase, there was no replacement during the breeding season. During the second, a peak year, females were replaced by individuals from adjacent habitats. This suggests that females may be more mobile during high numbers, possibly because of increased social interaction. It appears though, that the normal interactions between breeding females during increase years at least, are not sufficient to force animals to shift their home range to unoccupied areas.

This result is important in terms of answering the question of whether behavior can limit hare breeding densities. Watson and Moss (1970) outline four criteria that must be satisfied for this to be true. The most pertinent to this study is that a substantial portion of the population does not breed. This criterion is usually considered to be true if vacant areas created by experimental removal of breeding animals are filled

by other individuals which in turn breed. This is the case in red grouse (Jenkins et al. 1963) and in <u>Microtus</u> <u>townsendii</u> (Krebs et al. 1976).

Hares did not refill vacated areas created by experimental removal of females. This suggests that there were no individuals around that could increase their fitness by moving into those areas. In other words, there were no individuals present but not breeding because they did not have space to do so. However, this is negative evidence and as such is open to a variety of other possible explanations. The most obvious of these is that the removal of breeding females was done at the wrong time. Behavioral interactions may have sorted out which animals were going to breed at an earlier time. Losers may have died soon after and so were not available to colonize the removal area. If this were true though, one would expect to see an abrupt drop in survival when this behavioral organization occurred. This study detected no such drop. Further removal experiments at other times will be the only method of determining if there is a non-breeding surplus of animals at some time during the year or the cycle. The fact that Windberg and Keith (1976) did get animals moving into vacated areas in a peak year suggests that such a surplus may exist at this time.

Although females did not respond to the removal by shifting the location of their home range they did alter their actual use of of that range. If females avoid conspecifics, they would be expected to spend more time in the portion of their home range nearest the removal area and away from other females. This is what actually occurred. The fact that S.C.C. females showed no

similar shifts suggests that Telemetry females were responding to the removal and not to some other unknown factor.

The shift in home range use by Telemetry females was less pronounced after the second removal. Many of these had already shifted a large portion of their activity to the removal side of their home ranges after the first removal. It would be difficult then, for the animals to shift activity even more without actually moving the boundaries of their home ranges. As previously pointed out, females were unwilling to do this.

To conclude, female spacing behavior during the breeding season does not influence the actual location of an animal's home range. This seems to be set prior to the breeding season and subsequent changes in density have no effect. However, females responded to the removal experiment in a manner which suggests they utilize their home range in a way that avoids interaction.

7. EFFECT OF ADULT FEMALES ON JUVENILE MOVEMENTS AND SURVIVAL

One of the few common agreements among people working on small mammal population dynamics is the important influence of juvenile survival on changes in population numbers (Krebs and Myers 1974; Keith and Windberg 1978). However, the factors controlling juvenile survival are largely unknown. Keith and Windberg (1978) point to the influence of juvenile survival, particularly from summer to midwinter, on changes in snowshoe hare numbers. Survival they feel, is determined by the availability of woody browse in winter. However, the effect of the social milieu in which juveniles exist has not been examined. As a first step in this direction I examined the influence of adult females on juvenile movements and survival during fall and winter. Females have been shown to influence dispersal of juveniles in a number of species including pikas (Smith 1974), ground squirrels (Sherman 1977) and voles (Redfield et al. 1978).

I removed adult females from an area during the late breeding season and monitored juveniles on this area as well as on a control. This experiment allows a number of predictions from specific hypotheses to be tested. They include:

1. Females force juveniles to disperse into areas free of adults. If so this would be reflected by the removal area having:

(a) fewer juveniles dispersing

(b) greater rates of ingress

2. Females affect juvenile survival rates. Rates then,

should differ between control and manipulation areas.

3. Females influence use of an area by juveniles. This would be reflected by juveniles on the removal area shifting their home ranges after the manipulation.

No differences between the removal and control areas would indicate either that females were unimportant in determining juvenile survival and movements or that changes were not detected by my methods.

7.1. Methods

Juveniles were trapped on the two study areas, Telemetry and S.C.C.. Animals having a weight greater than 500 g were radio-tagged and located twice daily. Monitoring continued until Oct. 1st, 1978 after which animals were followed intermittently with intensive locating periods in late November 1978 and late February-March 1979. Grids were trapped weekly from May 1, 1978 to Oct. 1, 1978. Traps were also set once in October, twice in late November and weekly in March.

On August 14, 1978 the four adult females present on Telemetry were removed by trapping or shooting. The survival rates and movements of all juveniles caught at least once on either grid before the removal were monitored by trapping and telemetry. S.C.C. was used as an experimental control.

7.2. Results

7.2-1. Survival and Dispersl

A total of 32 juveniles were equipped with radio-collars. The fates of these animals after the removal can be seen in Table 11. Sexes were combined to increase sample size. There were no significant differences between the two grids in number still alive, number dying on the grid, or number dispersing. Also survival rates of all animals live-trapped at least once before the removal were not different between grids either (X^2, P > .05). There was some suggestion that the number of animals leaving Telemetry was higher (6 vs 3) but small sample sizes prevented meaningful comparisons.

The number of new animals caught on the grids after the removal was used as a measure of ingress. Results in Table 12 show that the number of ingressors was never significantly different on the two grids (X^2, P > .05). Results in Tables 11 and 12 then, provide no evidence that adult females influence the survival rate or long distance movements of juveniles during early fall to spring.

7.2-2. Changes in Home Range

The home ranges, as determined by telemetry, of five juveniles on S.C.C. and four juveniles on Telemetry were known before and after the removal. Figs. 24 and 25 show that there

TABLE 11

Fates of radio-tagged juveniles caught on S.C.C.
and Telemetry at least once before removal of adult
females. Figures cover time period from Aug 14-Mar 31 1979.

	S.C.C.	TELEMETRY
NO. ALIVE ON GRID	6	5
NO. DISPERSING	3	6
NO. DYING ON GRID	7	5
TOTAL	16	16

TABLE 12

Number of untagged animals captured on each
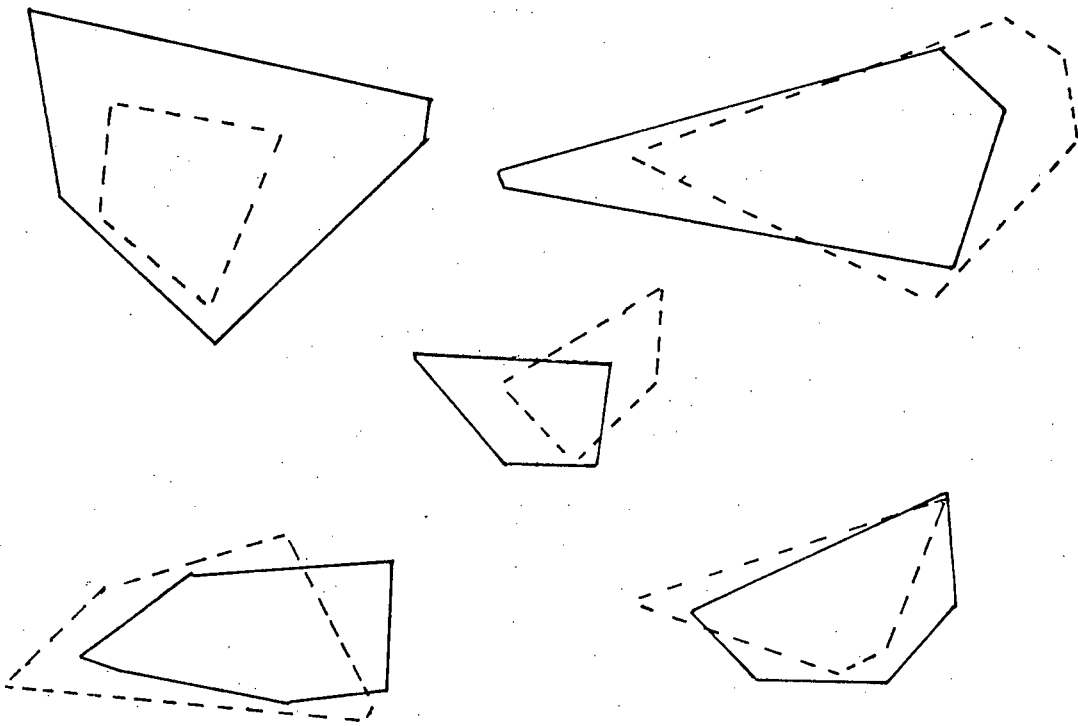grid after removal of adult females on Telemetry.

|	AUG14-OCT1/78		OCT1-DEC1/78		DEC1/78-MAR31/79	
	M	F	M	F	M	F
S.C.C.	12	11	4	4	4	0
TEL.	15	10	9	5	1	1

Figure 24.
    Home ranges of juvenile snowshoe hares on Telemetry showing
    no change in location before (---) versus after (- - -) the
    removal of adult females. Home ranges of individual animals
    are not in relation to each other.

85 m

Figure 25.
    Home ranges of juvenile hares on S.C.C. showing no change
    in location before (---) versus after (- - -) the removal
    of adult females on Telemetry. Home ranges of individual
    animals are not in relation to each other.
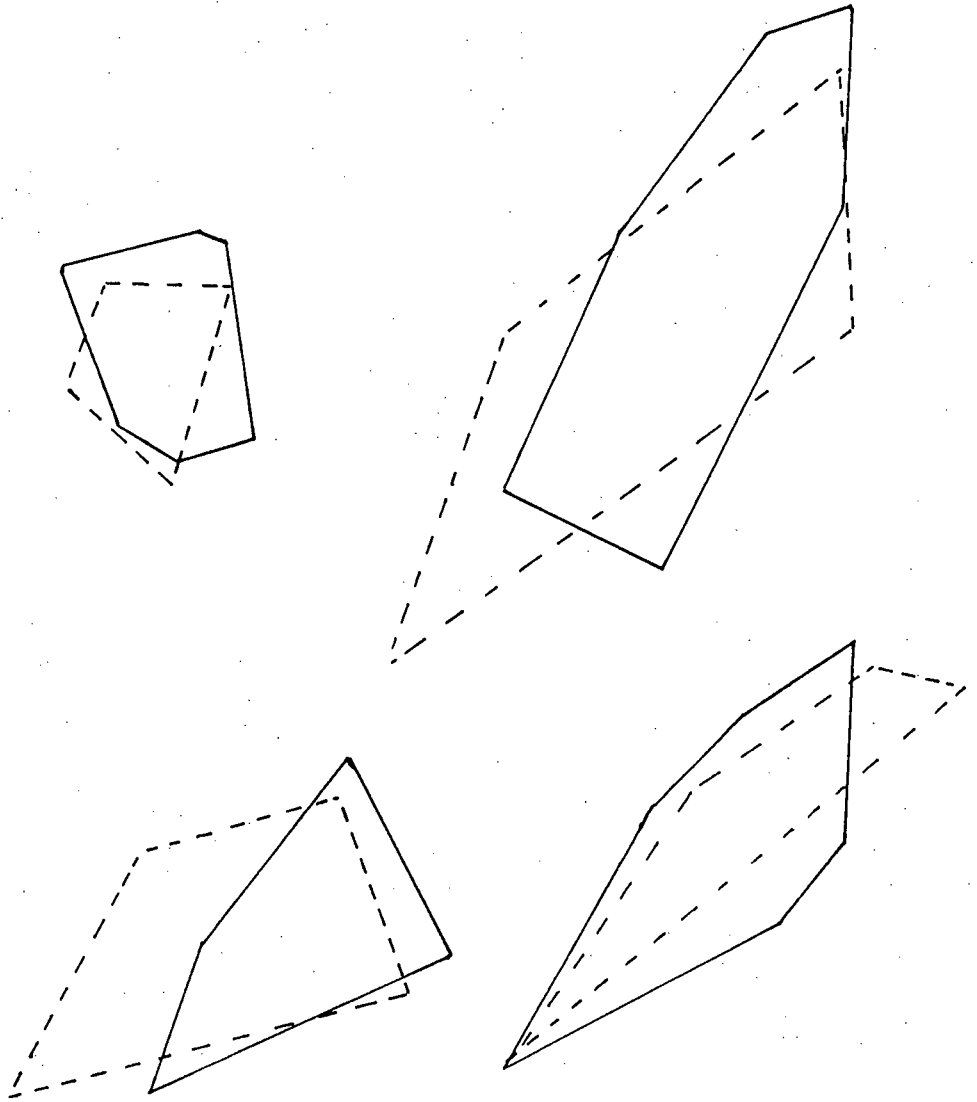
85m

were no shifts in any of these ranges following the
manipulation. Additionally, some knowledge of the whereabouts of
juveniles caught before the removal but not radio-tagged could
be determined by trapping results. These animals were later
radio-tagged and subsequent monitoring showed that their pre-
removal points of capture were never outside their post-removal
home ranges. The above suggests that removal of adult females on
Telemetry had no effect on movements of juveniles in that area.

However, changes in the amount of overlap between juveniles
and adult home ranges on S.C.C. suggests that some interaction
may have been occurring. Figs. 26 and 27 show the relative
locations of the trapping grids and juvenile and adult female
home ranges in both study areas prior to the removal. Juveniles
overlapped adults considerably in each case. There were major
differences in the location of adult females' home ranges
relative to the trapping grids. Females on Telemetry were
located directly on the grid while those on S.C.C. spent much
more time in the surrounding area. This situation was consistent
throughout the entire breeding season. Fig. 28 shows that
juvenile-adult overlap on S.C.C. decreased steadily throughout
late August and September. As more and more juveniles were
radio-tagged on the grid it appeared as though they were
avoiding areas occupied by adult females. Again, telemetry
showed no shift in home ranges to cause the decreased overlap.
Juveniles had already chosen the unoccupied areas by the time
they were first radio-tagged.

To summarize, there were no detectable differences in
survival rates or movements between juveniles on S.C.C. and

Figure 26. Relative locations of 5 adult female (---) and 5 juvenile (- - -) hcme ranges on S.C.C.. The trapping grid is represented by the dark lines. Notice the small proportion of adult ranges cn the grid.
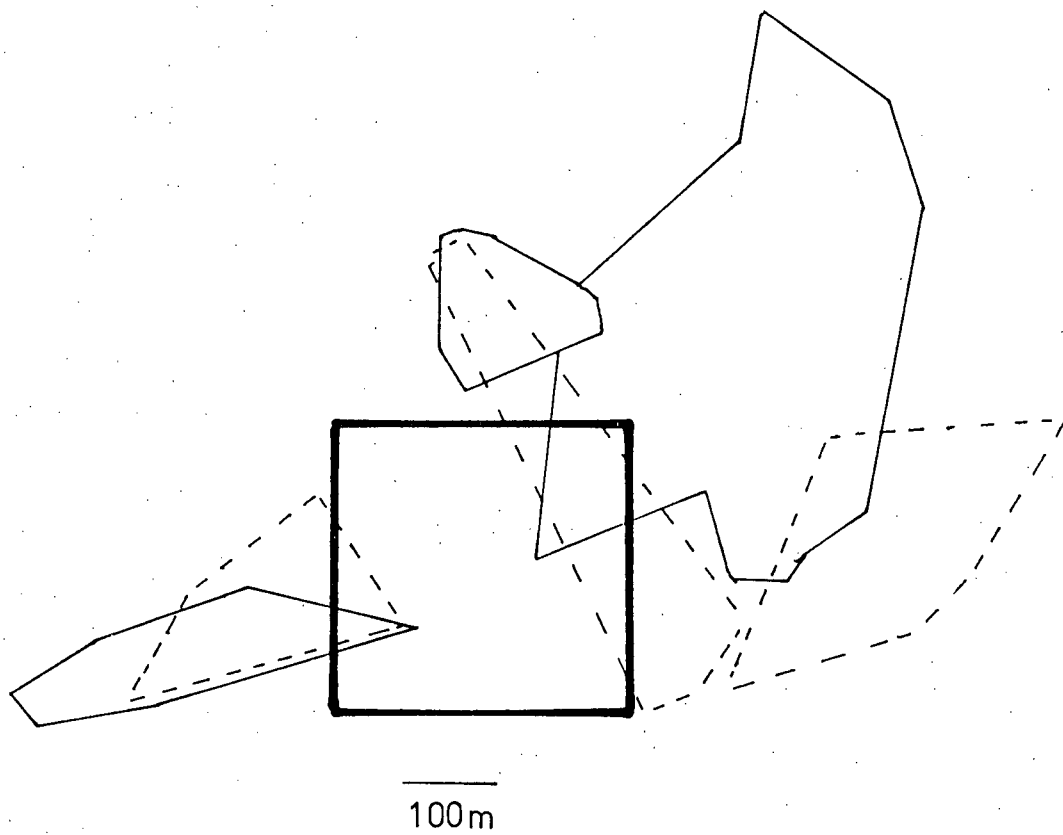
AUG 1-14 1978

100m

Figure 27. Relative locations of adult female (---) and juvenile (- - -) home ranges on Telemetry. The trapping grid is represented by the dark lines. Notice the central location of adult ranges relative to the trapping grid.
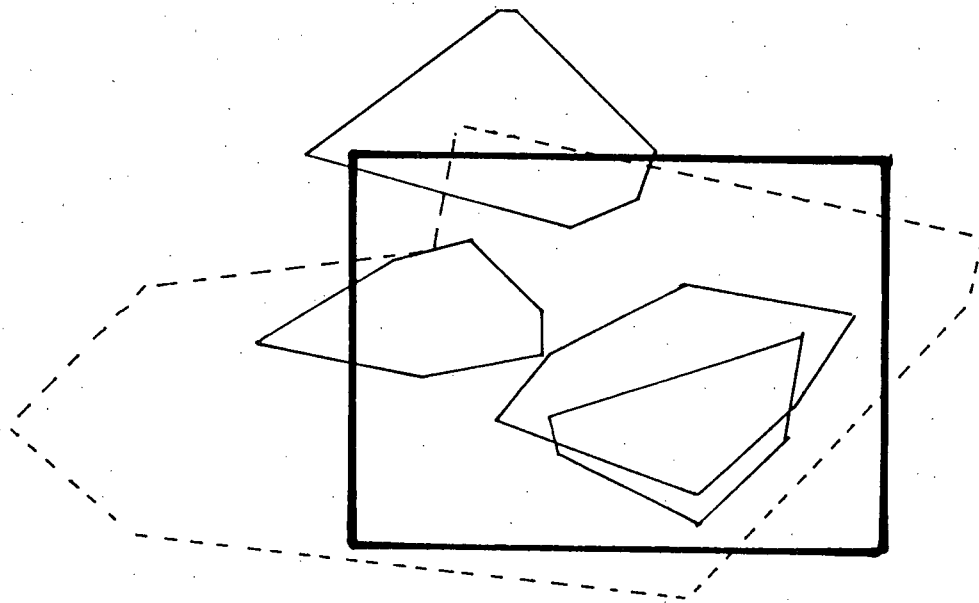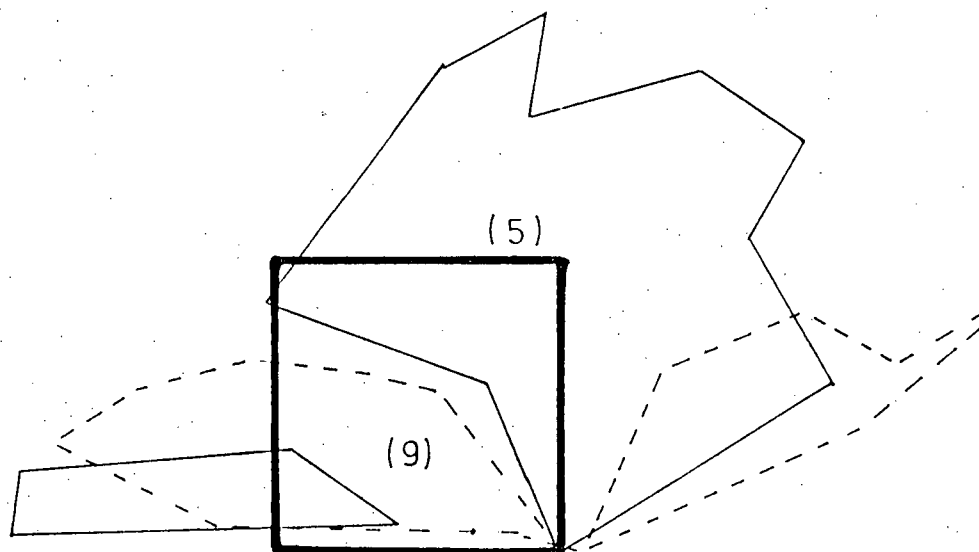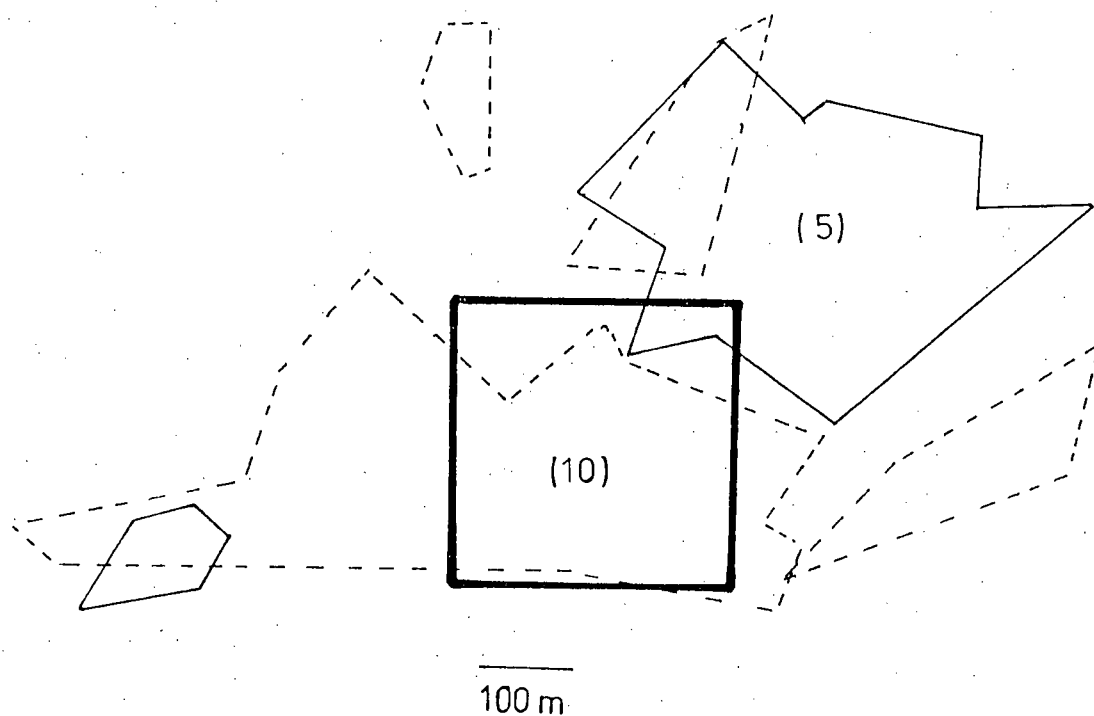
AUG 1-14 1978

50m

Figure 28.
    Home ranges of 5 adult females (---) and 10 (- - -)
juvenile hares on S.C.C. showing low overlap throughout
late August and September. The trapping grid is represented
by the dark lines.

AUG 15-31 1978

SEPT. 15-OCT. 1 1978

100 m

Telemetry after the removal of adult females on Telemetry. This suggests that adult females had little influence on these parameters. The small amount of overlap between juveniles and adults on S.C.C. however, indicates that the location of juveniles might be determined by females at a time prior to radio-tagging.

7.3. Discussion

Results of the above experiment indicate that females had no detectable effect on the survival and movements of juveniles during the late breeding season. The possible reasons for this outcome will now be discussed. The first of course, is that the above conclusion in correct. Other factors such as food (Keith and Windberg 1978) or adult male behavior (Healey 1967) may be more important at this time. It is also possible that female effects may become more important during peak and decline portions of the cycle. Removal experiments at this time would indicate whether this is so.

Females may influence juvenile movements each year but at times other than the late breeding season. In many mammals weaning is often a time when juveniles are forced to leave their parents' home range (Smith 1974). In this study the above is suggested by the fact that juveniles and adult home ranges on S.C.C. overlapped very little. Movements to reduce overlap, which initially must have been 100%, were done by juveniles since radio-telemetry revealed that adults did not shift their home range. As well, these movements had to occur before

juveniles were radio-tagged as no tagged animals showed shifts. The peculiar arrangement of adult females relative to the S.C.C. trapping grid created a situation where juveniles had to leave their mothers' home range before they could be captured. Later monitoring by telemetry then, merely revealed that they did not return once they had left.

The fact that home ranges of the two groups remained distinct suggests that some interaction was occurring even in late fall. Why then, did the experimental results show that adult females did not influence juvenile movements? The answer may be related to one of the underlying assumptions involved in the experiment. It was assumed that prior to the removal, juveniles and adults had overlapping ranges on both the experimental and control areas. Removal of adult females on Telemetry then, would create a situation where Telemetry juveniles were free from adult female interaction but S.C.C. juveniles were not. However, as shown in Fig. 26, S.C.C. juveniles occupied areas free of adult females. After the removal, juveniles on both grids existed in areas free of adults. Therefore neither group was experiencing pressure from females in the same area. As a result, even if adult females were important, the prediction of differences in juvenile movements between the two grids would not be born out.

It appears then, that the question of the importance of adult females on juvenile survival and movement during the fall and winter remains unresolved. Some juveniles leave their mother's home range at weights less than 500 g and come to occupy areas free of adult females. These two groups continue to

exist in distinct areas throughout the fall. Experiments involving removal of adult females earlier in the breeding season would provide answers as to whether juveniles are forced by females into these vacant areas or move on their own accord. Similarly, replication of the experiment in this study, but with a control area where the juveniles overlapped adult females, would provide more conclusive evidence as to the importance of adult females on juvenile survival and movement.

8. SPACING BEHAVIOR AND SNOWSHOE HARE POPULATION DYNAMICS

This study was designed to examine snowshoe hare spacing behavior, an aspect of the animal's ecology which has received little attention and could be important in understanding hare population dynamics. Three questions were posed at the outset of the study. They were:

1. What is the spatial arrangement of snowshoe hare home ranges?

Home ranges overlapped extensively between and within sexes throughout the year. Neither sex showed any type of territorial organization. It is possible that a dominance heirarchy is involved in mate selection and resource allocation .

2. Is female spacing behavior during the breeding season important in determining the location and use of neighboring animal's home ranges?

Changes in density did not affect the home range location of adult females. Animals were unwilling to shift their home range from areas of high overlap to areas vacated by removal of breeding females. However, females did use their home range in a manner that seemed to reduce interaction with neighbors.

3. Do adult females influence the movement and survival of juveniles?

The answer to this question is not clear. Experimental removal results suggested that adult females had no influence on

juveniles. However, the lack of overlap between juvenile and adult female home ranges during the fall suggests that some juveniles leave their parent's home range to occupy areas free of adults. This movement may occur prior to the time animals can be radio-tagged.

How do the above results relate to snowshoe hare population dynamics? This question is best examined in light of theories that attempt to explain the snowshoe hare cycle. The first and most prominent of these is that proposed by Keith (1974). He hypothesized that snowshoe hare cycles are caused by two interrelated predator-prey interactions. Firstly, as hares near peak numbers they begin to overbrowse their winter food supply. This overbrowsing causes damage to the plants and results in reduced plant growth. Food shortage for the hares results in lower rates of reproduction, adult, and juvenile survival. These combine to initiate the hare decline. Predator populations, which have built up with rising hare densities, act at this point to speed up and extend the decline phase. This allows the vegetation to recover but predator numbers, which decrease with lower hare numbers soon reach a point at which hare densities are allowed to increase once more.

The key to Keith's hypothesis is the hare-vegetation interaction. Spacing behavior is considered unimportant, possibly having a minor role in terms of intraspecific competition for food. If food supplies were abundant (eg. during increasing numbers) Keith's hypothesis would predict that spacing behavior should have little influence on home range location. In other words, if individuals were removed, as in

this study, there should be no replacement by surrounding individuals. Results from this study are in accordance with this prediction.

An alternative hypothesis to that of Keith would be one which incorporates behavior as an important component in snowshoe hare population dynamics. Watson and Moss (1970) outline a hypothesis whereby spacing behavior limits breeding densities by preventing some individuals from breeding. This hypothesis would predict that removal of breeding females should be followed by replacement with animals that otherwise would not have bred. Results of this study do not support the Watson and Moss (1970) hypothesis. However, the possibility still exists that numbers were limited at a time other than the one considered in this study. Perhaps this occurs during a season other than that studied here or possibly only during peak or decline phases of the cycle.

Another behavior hypothesis is that proposed by Chitty (1967) which also contends that numbers are limited by spacing behavior. Chitty goes on to point out that this behavior is under genetic control and subject to rapid selection. This means that during increasing numbers less aggressive genotypes are favored while in decline phases aggressive indivduals gain an advantage. One of the predictions of the Chitty hypothesis is that spacing behavior will be less intense during increasing as compared to declining populations (Krebs 1978b). This could possibly explain why females were not forced into the area created by the experimental removals in this study. Similar removals during peak and decline phases of the cycle are needed.

Work has shown that juvenile survival and movements are important to the population dynamics of snowshoe hares. The Keith hypothesis contends that changes in these factors are brought about by changes in food availability. The influence of spacing behavior remains unresolved. Results in this study suggest that some juveniles leave their parent's home range to occupy areas free of adults. Questions still remain as to the mechanism that causes these movements and whether dispersers experience survival rates similar to those individuals which remain in their parent's home range. Windberg and Keith (1976) postulated that juveniles dispersing during peak and decline years were forced to leave their initial home range because of intraspecific competition for food. However, it is difficult to believe that this occurs during periods of increase when food supplies are adequate. As pointed out by Lidicker (1975) dispersal might be a matter of choice rather than necessity during increase years. Alternatively, juvenile dispersal might be a function of adult aggressiveness which changes with phases of the cycle in a manner proposed by Chitty (1967).

Deciding between these alternative explanations requires a thorough knowledge of an individual's movements throughout its lifetime. Studies of dispersal to date have been hindered by the fact that the whereabouts of an individual are unknown for large portions of its lifetime. In the case of snowshoe hares nothing is known about individual movements between birth and the time of first trapping. As suggested by this study, important movements may occur during this time and because of present techniques, go unnoticed. These, as well as later long distance

movements must be taken into account if the relationship of dispersal to population dynamics is to be understood.

To conclude, this study serves as an initial investigation of snowshoe hare spacing behavior and its relation to the animal's population dynamics. As such, it has provided a better understanding of the spatial organization of hares and points to the need for continued work, especially in terms of the relationship of behavior to juvenile movements and survival. Results of experiments during the study fit the predictions of the Keith (1974) hypothesis more closely than they do alternate hypotheses incorporating behavior as a mechanism which limits numbers (Watson and Moss 1970). However, it must be stressed that this work examined behavior during only one phase (increase) of the snowshoe hare cycle. The possibility exists that spacing behavior could be very different during peak and decline years and suggests the need for continued examination of spacing behavior during these periods.

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