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Effect of late winter food addition on numbers and movements of snowshoe hares

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Summary. Peak (1980) and early decline (1981) populations of snowshoe hares were supplied with extra food in late winter to test the hypothesis that snowshoe hare populations are limited by food supply. Food supplemented populations increased through immigration in both years but the response was more pronounced in the early decline population. Animals supplied with extra food lost less weight, had higher survival in some cases, and males began to breed earlier. Immigrants to the food addition area were of two types: those that established home ranges on or near the area and those that spent only a brief time there before returning to their initial range. The possibility that these latter individuals were prevented from remaining on the food grid by residents is discussed. Results indicate that food supply is one factor that can limit peak and declining populations of snowshoe hares but the relation of spacing behaviour to food supply and numbers must also be considered.

Introduction

Populations do not increase without limit and much effort has been devoted to determining what factors are responsible for this limitation. For small mammals there is increasing experimental evidence that populations are limited by food (Taitt 1981; Taitt and Krebs 1981; Gilbert and Krebs 1981; Cole and Batzli 1978; Mares et al. 1982; Flowerdew 1973). When populations are supplied with extra food the usual response is a 2–3 fold increase in density through immigration, advanced breeding, and in some cases, improved survival.

These experiments indicate that food supply is one factor that determines the average density of small mammal populations. There is less evidence though, that food supply is responsible for changes in numbers within the same habitat over time. Food addition has not prevented declines in fluctuating vole populations (Desy and Thompson 1983). Snowshoe hares (*Lepus americanus*) fluctuate with a regular period of 9–10 years. Keith (1974) hypothesized that peak hare populations decline because they suffer winter food shortage which increases weight loss and lowers survival. Results of experiments in which enclosed populations were supplied with extra food support this hypothesis (Vaughan and Keith 1981). There is also some evidence that peak and early decline populations have relatively less food than populations at low levels (Pease et al. 1979). However, no one has reported results of supplying free ranging populations with supplemental food.

This study supplied free ranging populations of hares with supplemental food during late winter through early spring to test the hypothesis that snowshoe hare populations are limited by food. If so, populations should increase 2–3 fold. As well, if the Keith (1974) hypothesis is correct, food addition should decrease overwinter weight loss and improve survival of hares.

Recent studies have indicated that increased food supply can affect density by decreasing home range size which in turn, allows immigrants to settle in the population (Mares et al. 1976, 1982). I monitored changes in home range size of hares to determine if food addition 1) decreased home range size of residents and 2) if immigrants established home ranges on the food addition area.

Methods

Study area and experimental design

The study was conducted at Kluane Lake, Yukon Territory, Canada (61° North, 138° West Fig. 1). The vegetation is closed spruce (*Picea glauca*) boreal forest (Douglas 1974). Habitat surrounding the study areas is heterogeneous but all is used by hares except that immediately south of Silver Creek where a 250 m strip of bare ground exists. Radiotelemetry indicated that hares rarely crossed this area.

In 1980, snow covered the study sites until May 17 and hares did not have access to new leaves or herbs until the last week of May. These events occurred approximately one week later in 1981.

In 1980, the Telemetry trapping area received commercial (Buckerfields, 18% crude protein) rabbit chow from Feb. 29 to March 29 (Fig. 1). The chow was placed in ten 20 × 250 × 10 cm feeders which were distributed evenly over the grid. Similarly, on March 7 1981, chow was again placed on Telemetry as well as on a second grid, Grizzly. On March 30 the chow was shifted from the feeders to the traps themselves. Each trap was locked open and had 500 g of feed placed in it. During regular trapping sessions, the traps were set but not moved. Food was supplied to Telemetry in this manner until July 1 and to Grizzly until May 15.

Throughout the study I removed all animals caught from a fourth grid (Removal). The Removal was established in May 1979. Silver Creek and Telemetry had been trapped since May 1978, and Grizzly since May 1980.

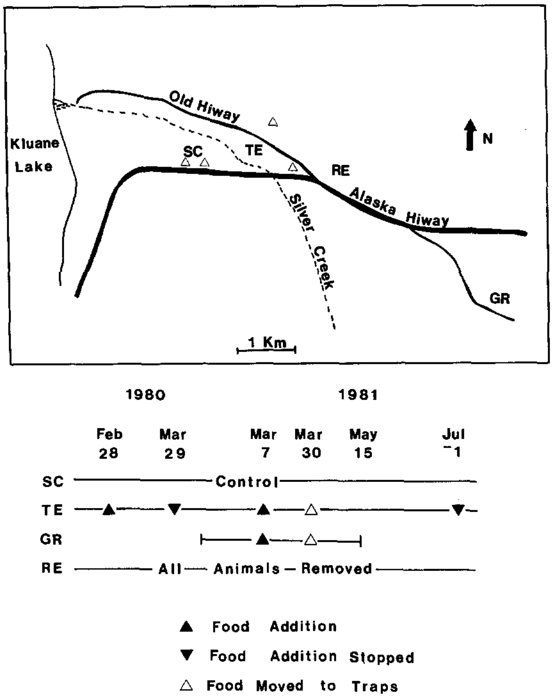

Fig. 1. Relative locations of study areas along the Alaska Highway near Kluane Lake, Yukon, Canada (61° N, 138° W). The experimental treatment each grid recieved is also shown. *SC* (Silver Creek) – control, *TE* (Telemetry) – food supplemented, *GR* (Grizzly) – food supplemented, *RE* (Removal) – all animals removed. Triangles represent locations of radio telemetry towers

Trapping

Each study site had a 300 × 300 m trapping grid with 100 stations arranged 30 m apart in a 10 × 10 pattern. Between 50 and 60 double or single door livetraps were placed at alternate stations. Traps were baited with alfalfa, set for two consecutive nights, and checked each morning. This was done every week in 1980 but was reduced to biweekly in 1981 to avoid trap deaths. Traps were locked open when not in use. The location, tag number, sex, reproductive condition, weight, and length of the right hind foot were recorded for each capture. 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. Males were classed as being in breeding condition if their testes were descended into scrotal sacks.

Populations size was determined by the complete enumeration (Krebs 1966) and Jolly (1965) techniques. Only complete enumeration values are provided because values from the two methods differed by an average of only 10%.

Telemetry

Hares on Silver Creek and Telemetry were fitted with radio transmitters weighing 30–45 g. The number of animals receiving radios depended on the availability of transmitters. Radios on each grid were located by triangulation from 2 permanent towers (Fig. 1). The true bearing of the radio from each tower was within ±1.5° of the recorded bearing 95% of the time (Boutin 1979). Each radio was located synchronously by two people, one at each tower. All locations were taken between 0600 and 2400. Between twenty and thirty locations were obtained every 2 weeks for each animal.

Table 1. Population size, as determined by minimum number alive, on the study areas from 1978–1981

Grid	May 1978	February 1979	February 1980	February 1981
Silver Creek	8	15	59	26
Telemetry	7	16	58	28
Grizzly				54

Home range size was determined by the minimum polygon method (Hayne 1949). I modified this technique to include only 90% of the total number of locations for each animal. Locations farthest from all others were excluded. Locations falling in a region where error polygon length (Heezen and Tester 1967) was greater than 75 m were disregarded. Any animal with greater than 20% of its locations in this zone was not included in the analysis because locations were not considered accurate enough to determine home range size. I determined home range size of only those animals for which I had 15 or more locations during the period of analysis.

Results

Changes in numbers

The effect of food addition on hare numbers may depend on population density. Table 1 shows that February numbers on Silver Creek and Telemetry increased each year from 1978 until 1980 and then declined. Numbers in February 1981 were half those in March 1980. Trapping on Grizzly did not cover a long enough period to determine when hare numbers on this area reached a peak. In February 1981, numbers on Grizzly were twice that on Telemetry and Silver Creek. Telemetry received supplemental food then, in the winters of peak (1980) and early decline phases (1981) of the cycle.

Did numbers increase on the experimental grids? Changes in numbers after food addition varied between sexes and between years (Figs. 2, 3). During food addition in 1980, the number of males on Telemetry reached levels 1.4 times higher than that on Silver Creek. This difference decreased to 1.2 times after food addition stopped and was zero by early May. The number of females on Telemetry was slightly above that on Silver Creek throughout the food addition period.

In February 1981, numbers on Silver Creek and Telemetry were again equal, but half that of one year before. During food addition to Telemetry, male and female numbers increased while those on Silver Creek remained constant. Numbers were three times higher on Telemetry than on Silver Creek for both males and females. The number of hares on Telemetry in May 1981 was slightly higher than that present one year earlier.

Prior to food addition, the number of males on Grizzly was twice that on Silver Creek. During food addition, male numbers increased briefly in early April but declined overall and remained double those on Silver Creek. The number of females on Grizzly prior to food addition was slightly less than on Silver Creek but was twice as high during food addition.

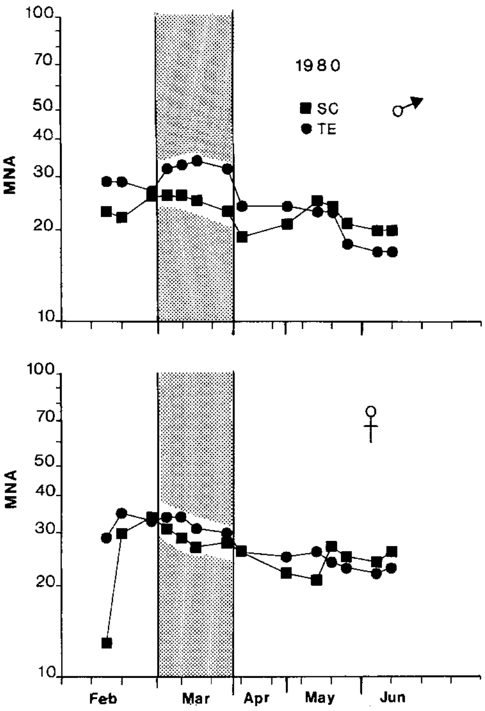

Fig. 2. Changes in population size, as determined by Minimum Number Alive (*MNA*) on the study areas in 1980. *SC*, control; *TE*, food addition. The shaded area represents the period when supplemental food was present on TE

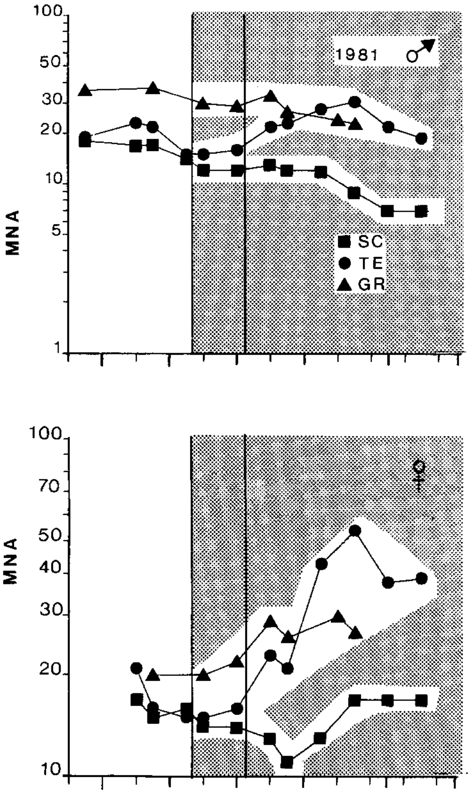

Fig. 3. Changes in population size, as determined by Minimum Number Alive (*MNA*), on the study areas in 1981. *SC*, control; *TE* and *GR*, food supplemented. The shaded area represents the period when supplemental food was present on the food addition grids. The vertical line represents the point when food was shifted from large feeders to the traps

Table 2. Number of immigrants (animals trapped for the first time) caught each month on the study areas. Telemetry and Grizzly received supplemental food

Grid	February		March (food present)		April		May	
	M	F	M	F	M	F	M	F
1980								
Silver Creek	17	30	3	4	5	8	7	9
Telemetry	11	27	12	4	2	7	7	14
Removal	19	15	34	28	37	35	13	21
1981			(——— food present ———)					
Silver Creek	5	2	0	1	3	2	2	9
Telemetry	12	5	3	2	15	34	10	34
Grizzly	8	6	1	4	8	11	9	25
Removal	19	34	8	6	37	39	18	36

To summarize, during food addition, numbers of males in 1980, and males and females in 1981, were higher on Telemetry relative to that on Silver Creek. Food addition to Grizzly did not change male numbers relative to those on Silver Creek but increased female numbers.

Immigration

The increase in numbers on the experimental food areas could be due to increased immigration or survival. I first examine immigration. New animals tagged each trapping session were classed as immigrants. This assumes that these individuals were not living on the grid and avoiding capture. Immigration to the food grids varied between years (Table 2). In 1980, the total number of male immigrants to Telemetry during the food addition period was significantly higher than that to Silver Creek (12 vs. 3, chisquare = 4.26, Yates correction factor, df = 1, $P < 0.05$). The number of female immigrants to Telemetry and Silver Creek did not differ. The number of immigrants caught on Telemetry was well below the number of animals caught on the Removal throughout March, April, and May.

During the food addition period in 1981, the number of immigrants to the experimental grids was much higher than that to Silver Creek (Table 2). A total of 28 males immigrated to Telemetry during the food addition period as compared to 18 on Grizzly and 5 on Silver Creek. This was still less than half the number of males (63) caught on the Removal over the same period. Seventy females immigrated to Telemetry during the food addition period as compared to 40 on Grizzly and 12 on Silver Creek. A total of 81 females were captured on the Removal.

To summarize, food addition increased immigration of males to the food grids in 1980 and 1981. The number of female immigrants to the food grids increased in 1981 only.

Survival

I next asked if food addition improved survival of resident hares. I defined residents as any animal caught at least once prior to the food addition period. The recapture rate of marked animals can be used as an index of survival. It is a minimum estimate because emigrants are considered as losses. There were no differences in survival between

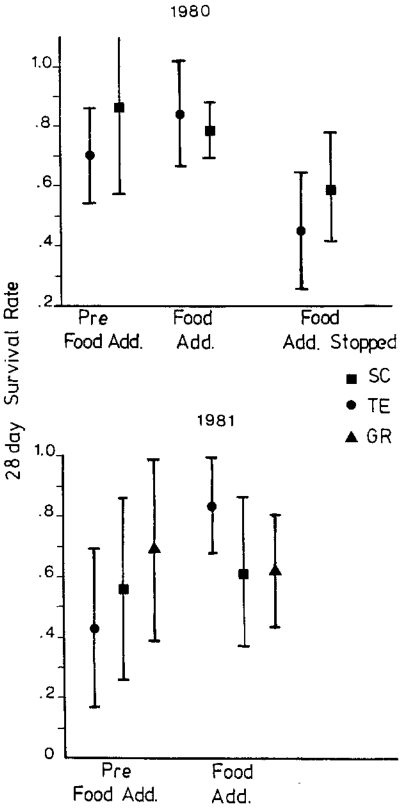

Fig. 4. Mean minimum 28 day survival rates, as determined by recapture of tagged hares, for animals on all study areas. *SC*, control; *TE* and *GR*, food supplemented grids. Narrow bars represent 95% confidence limits

Table 3. Mean net weight change of hares caught both one week prior to and one week after food addition. In 1980 this was equivalent to a 4 week period and in 1981 it was a 6 week period. Sample sizes are in brackets

Grid	1980 Males	1980 Females
Silver Creek	−152.73 (11)	−131.89 (9)
Telemetry	−111.25 (12)	+ 12.0 (10)**
	1981 Males	1981 Females
Silver Creek	−103.89 (9)	− 23.50 (3)
Telemetry	− 67.5 (8)	+111.00 (5)***
Grizzly	− 69.44 (9)	+43.75 (4)**

**$P<0.01$; ***$P<0.001$, t-test comparison between control (Silver Creek) and experimental (Telemetry and Grizzly) grids

sexes so the data are lumped. Survival of hares on Telemetry improved after food addition in each year (Fig. 4). The difference was significant in 1981 (t-test, $t=3.54$, df$=14$, $P=0.003$). During the food addition period in 1980, survival of hares on Silver Creek decreased and in 1981, it improved only slightly (0.56 to 0.61). Survival of hares on Grizzly did not improve after food addition.

Weight loss

Keith and Windberg (1978) hypothesized that overwinter weight loss of hares is related to food availability. To test this, I measured the change in weight of hares trapped both one week prior to food addition and one week after food addition had stopped. In 1981, because food addition continued for a longer period than in 1980, I used weights of animals caught in mid to late April rather than those of animals caught after food addition stopped. Weight changes of animals then, are for a period of 4 weeks in 1980 and 6 weeks in 1981. Table 3 shows that females on the food grids lost significantly less weight than those on Silver Creek. Males on the food grids also lost less weight than those on Silver Creek but the difference was not significant.

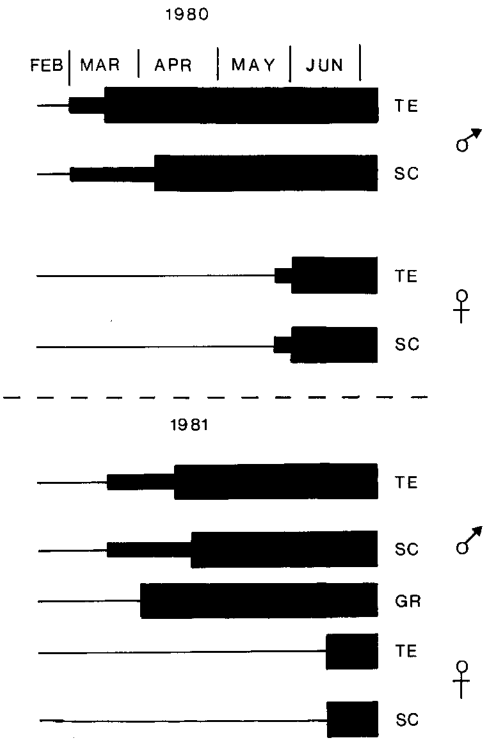

Fig. 5. Onset of breeding in male and female hares on each of the study areas. Males were considered to be in breeding condition if their testes were descended into scrotal sacks. Females were considered to be in breeding condition if they were lactating. Narrow bars mean that no animals captured were in breeding condition. Intermediate bars mean between 1 and 50% were in breeding condition. Wide bars mean greater than 50% were breeding

Onset of breeding

I next asked if supplemental food could cause snowshoe hares to begin breeding earlier. The onset of breeding in males was defined as the time when greater than 50% of the males had scrotal testes. Males on the food grids came into breeding condition earlier than did those on Silver Creek (Fig. 5). In 1980, greater than 50% of the males were breeding on Telemetry 3 weeks before the same situation occurred on Silver Creek. In 1981 onset of breeding was one week earlier on Telemetry and 3 weeks earlier on Grizzly. Supplemental food did not change the time at which females gave birth (Fig. 5).

Home range size and dispersal

To test if home range size changed with food supply, I compared home range size of radio-collared resident hares before, during, and after food addition. Only those animals caught at least once prior to the food addition period (residents) were included in the analysis. Males and females were lumped because size of their home ranges did not differ significantly. Residents on Telemetry decreased their home range size in 1980 after food addition (*t*-test, $t=3.18$, $df=26$, $P=0.003$, Fig. 6). In 1981, they did so in May only (*t*-test, $t=2.04$, $df=24$, $P=0.05$) but this seemed due to season rather than the presence of food as hares on Silver Creek also decreased home range size in May (*t*-test, $t=2.20$, $df=15$, $P=0.03$). It seems then, that resident hares responded to increased food by decreasing home range size in 1980 but not in 1981.

I next asked if radio-collared resident hares with supplemental food were less likely to disperse than those with normal food. An animal was considered to have dispersed if it moved to occupy a home range that did not overlap with the one it occupied when first radio-collared. The proportion of residents which dispersed was the same each year so I lumped data from both years. Three of 36 radio-collared residents dispersed from Silver Creek. This compares with 5 of 41 dispersing on Telemetry. The addition of food did not alter dispersal rate of residents.

Use of the food addition area

To determine if hares provided with supplemental food increased their use of the food addition area, I compared the proportion of radio locations found on Telemetry before and during food addition. In 1980 the average proportion increased from 0.20 to 0.28 (*t*-test, $t=3.18$, $df=36$, $P=0.003$) when food was added (Fig. 7). After food addition stopped, the proportion dropped to 0.27. In 1981 hares did not increase their use of the food addition area (Fig. 7).

I also compared use of the food grid by residents with that of animals caught after food was added. The two groups did not differ in their use of the food addition area (*t*-tests, $P>0.05$), indicating that residents and immigrants had equal access to the food addition area.

Movements of immigrants

I next tried to determine if immigrants caught on Telemetry in 1981 were animals that shifted their home range to the food grid completely or whether they merely expanded their existing range to include the food addition area. If the latter is true, the observed increase in numbers would reflect an increase in relative trapping area rather than in actual density. If the above is true, immigrants should have had larger home ranges than residents. This was not the case at any time during the food addition period (*t*-tests, $P>0.05$). I then compared the location of resident and immigrant home ranges relative to the grid. To do this, I calculated the distance from the arithmetic centre of each home range to the centre of the trapping grid. Home ranges located in areas where the error polygon length of locations was greater than 75 m were assigned values of 500 m. Mean distances of residents and immigrants from the grid were not significantly different (*t*-test, $t=1.55$, $df=21$, $P>0.05$). However, the frequency distribution of distance from the grid for each group differed (Fig. 8). Home ranges of residents had a unimodal distribution. Only one animal was located greater than 500 m away. In contrast, the frequency distribution of distance of immigrants from the grid was

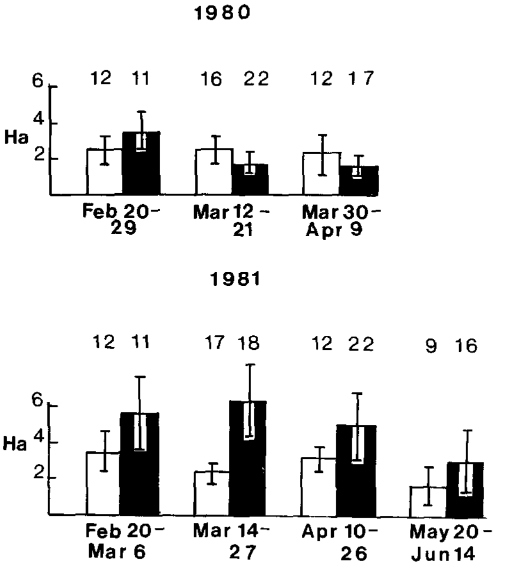

Fig. 6. Changes in average home range size of radio-collared resident (animals caught at least once before food was added) during the study. Wide bars are mean values and narrow bars represent 95% confidence limits. Open bars are for animal on Silver Creek (control). Dark bars are for animals on Telemetry (food supplemented). Sample sizes are placed above each bar. Supplemental food was present on Telemetry during the March 12–21 period in 1980 and from March 14 onwards in 1981

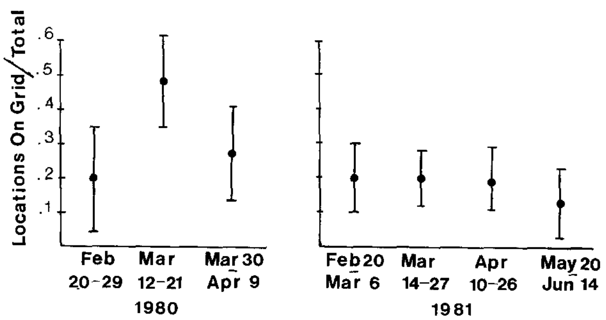

Fig. 7. Use of the food addition area by animals radio-collared on Telemetry. Use was determined by the proportion of all locations that were on the trapping grid. Dots represent mean values and narrow bars are 95% confidence limits. Supplemental food was present on Telemetry during the March 12–21 period in 1980 and from March 14 onwards in 1981

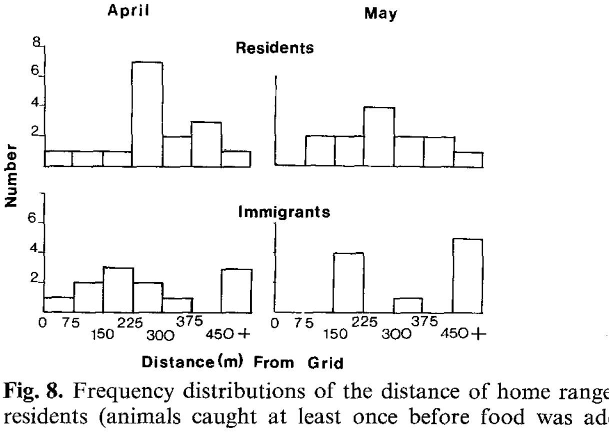

Fig. 8. Frequency distributions of the distance of home ranges of residents (animals caught at least once before food was added) and immigrants (animals caught for the first time after food was added) from the trapping grid during April and May 1981

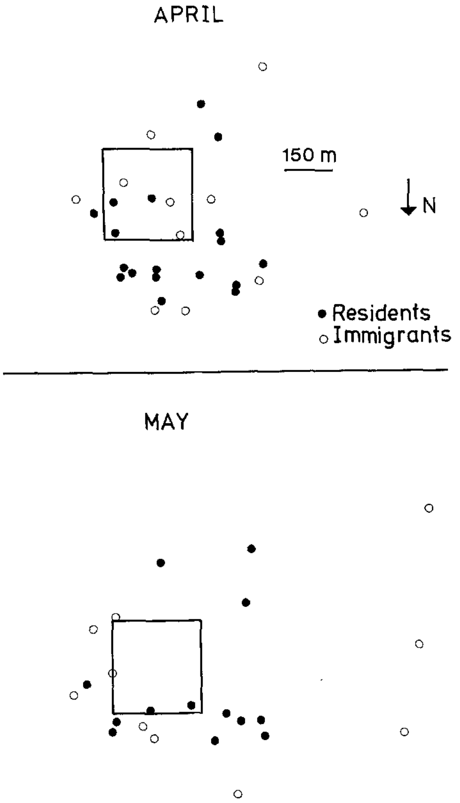

Fig. 9. Relative locations of the arithmetic centres of home ranges of residents and immigrants with radio-collars on Telemetry in April and May, 1981. The large square represents the location of the trapping grid

bimodal (Figs. 8 and 9). Of the 20 immigrants for which sufficient information was obtained to determine home range location, 12 settled within 500 m of the grid. Of the 8 that settled farther away, 4 were trapped only once and none of these were trapped in May. Further, of the 52 female immigrants caught in late April to early May, 23 were captured only once. It appears then, that immigrants were not animals which expanded their ranges to make regular visits to the grid after food was added. However, there appeared to be two types of immigrants; those that actually settled on or near the food addition area and those that made only brief forays to the grid before either returning to or moving to areas well off the grid. Immigrants that did remain near the food grid had movements similar to residents.

Did immigrants remain on the food grid after food addition stopped? In 1980, only one of 16 immigrants was caught after food addition was stopped. In 1981, only 35 of 98 immigrants were retrapped after food addition stopped.

Discussion

Gilbert and Krebs (1981) proposed that the usual response of small mammal populations to food addition is to double in numbers and that we should look for instances where this does not occur. Is this the case for snowshoe hares? Increased immigration led to higher numbers on the food grids in both years but the degree of response differed between years. One possible explanation for the difference is that food was less limiting in 1980. Natural food supplies may have been barely adequate in 1980 but heavy browsing could have reduced food to inadequate levels in the following year (Keith and Windberg 1978). That food was in short supply during the 1980 food addition period is suggested by the following observations. During the food addition period, bait left in the traps after the regular trapping session disappeared rapidly on Silver Creek but often remained on Telemetry until the next session. As well, a second check of traps in the afternoon of the first day of trapping produced as many as 15 animals on Silver Creek but none on Telemetry. This high number of captures is unusual as hares are normally inactive during the day and it suggests that the bait was important enough for the hares to shift their activity patterns.

A second possibility is that the animals themselves differed in aggressiveness between years (Chitty 1967). Hares may have been more aggressive in the year of peak numbers and consequently were able to exclude immigrants from settling. In the first year of decline however, surviving individuals may have been less aggressive and so unable to prevent immigration. However, this is contrary to the Chitty Hypothesis which predicts that animals should be relatively more aggressive in the decline than in the increase and peak phases of the cycle.

A third possibility is that the response to food addition was density related. Numbers on Silver Creek and Telemetry, prior to food addition in 1980, were twice that in 1981 (Figs. 3, 4). The 1980 levels may reflect a limit set by spacing behaviour, with the result that additional food produced only a slight increase. Similarly, male numbers on Grizzly began at levels equal to those on Silver Creek and Telemetry in 1980 and again showed no increase in numbers after food addition. However, other factors may have influenced the results from Grizzly. Trapping success was reduced by: 1) a moose in the area frequently setting off traps while attempting to get at the feed and 2) hares may have avoided traps because of frequent visits by lynx hunting in the area. Immigration of males to Grizzly was higher than to Silver Creek and total numbers may have been higher if not for the above complications.

A fourth explanation for the differences in response to food addition in 1980 versus 1981 is that immigrants may have been untrappable in 1980. They may have been present on the food grid but avoided traps because they had access to food at feeders. This is supported by results in 1981, when immigration did not increase on Telemetry or Grizzly until food was placed in traps (Table 2), even though supplemental food had been available a full 3 weeks earlier.

Further experimentation is needed to differentiate between the above possibilities. At present one can only say that short term food addition can increase numbers of hares 2–3 fold during the early decline phase of the cycle and may also do so during the peak phase.

Supplemental food decreased weight loss and improved survival of both sexes, and advanced onset of breeding condition in males in both 1980 and 1981. The only exception was that survival on Grizzly did not improve with food addition. This may have been due to high rates of lynx predation in the area. Tracks of at least two animals were regularly seen on the grid whereas lynx tracks were seldom seen on the other areas. Vaughan and Keith (1981) provided supplemental food to hare populations in large enclosures.

Theirs was a long term food addition but results were similar to this study. Empirical evidence collected over 15 years has led Keith and Windberg (1978) to hypothesize that overwinter food shortage is the critical factor initiating snowshoe hare declines. Results from this study indicate that food supply can affect survival and weight loss of hares in free ranging populations. Further, food addition on Telemetry in 1981 restored breeding numbers to above the peak levels present in 1980. This suggests that the change leading to the decrease in numbers between 1980 and 1981 was food related. This may have been a direct habitat change or a change in the animals' ability to survive on a given amount of food.

Home range size

Food addition has been found to lead to a decrease in home range size in deermice (Taitt 1981), voles (Taitt and Krebs 1981), and chipmunks (Mares et al. 1976, 1982). Mares et al. (1982) have shown that reduced home range size is due to food addition rather than the concomitant increase in density. Taitt (1981) postulated that it is the reduction in home range size that allows immigrants to enter a food supplemented population. In chipmunks, residents contracted their home range after food addition and immigrants settled in areas no longer used by residents. After food addition was stopped, residents forced immigrants to emigrate (Mares et al. 1976).

In this study, food addition led to a decrease in home range size in 1980 but not in 1981. A decrease in home range size then, was not necessary for hare numbers to increase. Hares form dominance heirarchies and have home ranges that overlap extensively (Graf 1981; Boutin 1979). It seems that the ability of dispersers to recruit to populations with a social system of this type is less dependent on changes in home range size than it is in the more site exclusive system of chipmunks (Mares et al. 1976) and voles (Madison 1980).

Why did hares on Telemetry reduce their home range size in 1980 but not in 1981? Hares with supplemental food may still require natural browse to obtain an optimal diet. In 1980, the natural browse available on Telemetry may have been such that hares could contract their range and still obtain their requirements. Browsing in the year of peak densities may have altered the vegetation enough to make this impossible for hares in 1981.

It is also possible that predation pressure may have influenced the home ranges size of hares on Telemetry in 1981. Predation pressure appeared higher in 1981 than in 1980. Predators were responsible for killing 6 of 23 resident radio collared hares on Silver Creek in 1981 versus 2 of 14 in 1980. Keith and Windberg (1978) also found that predation pressure was higher in post peak versus peak years. Wolff (1980) argued that hares chose habitats which afford protection from predation in post peak years. In 1981, hares on Telemetry spent considerable time off the trapping grid in areas of thick immature spruce and willow. This may have been to avoid predation and hares were unwilling to shift to the more exposed food addition area as evidenced by the lack of increase in use of the food addition area in 1981.

These explanations are speculative, but they can be tested. Supplemental food could be added to a grid and natural food and cover could be increased by cutting large spruce trees. Home ranges of hares in this area should decrease in size after the manipulation.

Emigration and immigration

This study confirms Wolff's (1980) contention that food supply is an important factor in determining movement of hares between habitats. Food addition increased rates of immigration but did not alter emigration rates. Dobson (1979) obtained similar results in Californian ground squirrels. However, emigration in this study was low on both Silver Creek and Telemetry. A better test of the effect of food supply on emigration rates would be to reduce rather than increase food supply.

Along with the increase in immigration with food addition there was also a seasonal increase to all study areas in mid April to early May. The number of animals caught on the Removal increased from less than 20 per trapping session to as high as 35 per session. Similarly, immigration to Silver Creek went from near zero to as high as 6 animals in one session. Mid-April coincides with the period when the first litters are conceived and the above probably reflects increased movement by animals searching for suitable breeding spots. The increase in movement in April 1981 was much more pronounced than in 1980. As well, in 1981, females were moving more than males whereas males and females were moving equally in 1980. I suggest that the difference between years was due to the relative availability of food in each year. In April 1980, food supplies were sufficient to support most of the hares present on the study areas. As a result, the increase in dispersal at this time was relatively small. In contrast, relative food supply was lower in 1981. Consequently, Telemetry, because food was added, and the Removal, because the relative browsing pressure on the area was reduced by removal of animals, represented areas of favorable food supply. This served to attract hares to both areas. The higher response of females was probably due to increased energy demands relative to males, because they were starting to produce embryos. Females then, are probably more sensitive to energetic constraints at this time while males are more concerned with obtaining females to mate with. Taitt (1981) reached similar conclusions for deermice.

I think the removal area and food addition grids actually attracted animals in 1981 for the following reasons. Firstly, the increase in dispersal, indicated by the increase in number of captures on the removal grid, was not reflected in an increase in dispersal of radio-collared animals on Silver Creek. Secondly, a large number of immigrants to Telemetry during May were captured only once. I suggest that these and radio-collared immigrants were animals that left there original home range to occupy the food grid only briefly before returning to home ranges located well off the grid (Fig. 9). Most did not remain on the food grid; possibly because residents prevented them from doing so. It seems then, that hares normally increase their movements in April. However, animals do not necessarily disperse at this time but may make forays off their range in search of unoccupied habitat. If they are unable to find favorable spots they return to their original home range. In 1981, when food supply was relatively low, the apparent amount of movement was exaggerated by both Telemetry and the Removal because they represented areas of favorable food supply. Animals reaching these areas remained long enough to be captured at least once and some actually established home ranges on or near the grid. Food availability then, is one factor that determines where hares will settle in spring and in so doing, can limit density at this time. Not all immigrants remained in the area though, possibly because residents prevented settlement. In previous experiments I tried to alter spring breeding densities of females by altering spacing behaviour (Boutin 1980). They were unsuccessful. However, from findings in this study, the experiments may have been done after the period of spring reorganization and so were ineffective. As well, the experiments were done during the increase phase of the hare cycle. The relative importance of spacing behaviour in determining hare movements and density in an area may change with phases of the cycle as might the importance of food availability and spacing behaviour of animals in surrounding habitats. Experiments involving both factors during various phases of the cycle are required if we are to fully understand how they influence snowshoe hare population dynamics.

To conclude, supplemental food in late winter decreased weight loss and improved survival in hares as predicted by the Keith (1974) hypothesis. Food availability can limit numbers in spring but the effect of initial densities on the response of hare numbers to food remains unclear. Not all animals that enter an area with supplemental food remain there. Some appear to return to their initial home range. This may be due to residents on the food addition area preventing them from remaining.

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