The role of dispersal in the population dynamics of snowshoe hares

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Received April 16, 1984

BOUTIN, S., B. S. GILBERT, C. J. KREBS, A. R. E. SINCLAIR, and J. N. M. SMITH. 1985. The role of dispersal in the population dynamics of snowshoe hares. Can. J. Zool. **63**: 106–115.

We monitored dispersal of snowshoe hares (*Lepus americanus*) at Kluane Lake, Yukon, during a population increase, peak, and decline. Dispersal was measured by recording the number of immigrants to a removal grid and by tracking radiocollared individuals. The observed decline was not due to dispersal, as a maximum of 28% of all losses of radiocollared animals was due to dispersal. Dispersal rate (as measured by number of immigrants to the removal grid per individual on the control grid) was negatively correlated (−0.51, *P* < 0.01) with the rate of population increase. Highest dispersal rates occurred in the winters when hare populations were at peak and early decline densities. Dispersers at this time were lighter in weight than residents. We discuss our results in light of current hypotheses attempting to explain dispersal in cyclic small mammals and conclude that our results are consistent with the hypothesis that food shortage is responsible for increased rates of dispersal at peak population densities Comparison of dispersal, as monitored by radiotelemetry, versus immigration to a removal grid, suggests that removal grids overestimate dispersal, particularly at high densities when removal grids may attract animals because food supplies are relatively favorable there.

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La dispersion des lièvres (*Lepus americanus*) a fait l'objet d'une étude chez une population de Kluane Lake, dans le Yukon, durant la croissance, le climax et le déclin de la population. La dispersion a été mesurée en notant le nombre d'immigrants dans une aire d'où étaient retirés les résidants et en suivant des individus munis d'un collier à émetteur radio. Le déclin de la population n'était pas attribuable à la dispersion, puisque 28% au maximum des pertes d'animaux munis d'un émetteur étaient dues à la dispersion. Le taux de dispersion (mesuré en termes de nombre d'immigrants aux aires de retrait par individu dans l'aire témoin) était en corrélation négative (−0,51, *P* < 0,01) avec le taux d'accroissement de la population. Les taux de dispersion maximaux ont été enregistrés en hiver, alors que les populations étaient à leur densité maximale, et au début du déclin. Les émigrants à ce moment étaient de masse moins grande que les animaux résidants. Les résultats sont examinés à la lumière des hypothèses courantes sur la dispersion des petits mammifères cycliques; les résultats s'accordent avec l'hypothèse qui veut que la pénurie de nourriture soit responsable des taux plus élevés de dispersion aux densités maximales de population. La comparaison entre les résultats obtenus par le retrait des résidants et les résultats obtenus chez les individus munis d'un émetteur révèle que la méthode du retrait des résidants entraîne une surestimation de la dispersion, surtout aux densités élevées, car les aires ainsi vidées sont susceptibles d'attirer des animaux, puisque les réserves de nourriture y sont relativement plus abondantes.

[Traduit par le journal]

Introduction

Population size and composition are dependent on inputs from births and immigration and outputs from deaths and emigration. Immigration and emigration have usually been considered equal and thus unimportant in causing population change. This view is no longer acceptable (Lidicker 1962, 1975; Krebs and Myers 1974) and to understand a species' population dynamics we must analyze dispersal (Watson and Moss 1979). Evidence that dispersal is necessary for population regulation comes from studies in which it has been artificially eliminated. Krebs et al. (1969) found that enclosed populations of *Microtus ochrogaster* and *Microtus pennsylvanicus* reached abnormally high densities and destroyed the habitat. However, the actual mechanism by which dispersal is involved in population regulation is unclear (Gaines and McClenaghan 1980). Theoretically, dispersal could account for the major declines observed in fluctuating populations, but empirical observations suggest that this is not the case (Beacham 1980; Hilborn and Krebs 1976; Windberg and Keith 1976). However, the technical difficulties involved in identifying and following dispersers (use of removal grids to enumerate dispersers) do not preclude the possibility that long-range dispersers may have been missed.

The snowshoe hare (*Lepus americanus*) is a boreal forest herbivore whose numbers show cyclic fluctuations (Keith 1963). We monitored dispersal of hares during an increase, peak, and decline in population to determine how it is involved in the regulation of hare numbers. Four hypotheses have been proposed that incorporate dispersal as part of a mechanism that explains cyclic population fluctuations. Before examining these hypotheses, it is important to clarify the meaning of dispersal rate. We define it as a per capita rate expressed as the number of dispersers per individual in the population. Keith (1974) hypothesized that snowshoe hare population declines are initiated by overwinter food shortage and dispersal rates are increased because animals are forced to vacate areas of inadequate food supply (Windberg and Keith 1976). This hypothesis predicts (*i*) that dispersal rate should be highest when hares reach peak density and food supplies become inadequate and (*ii*) that dispersers should be in poorer physical condition than residents.

Wolff (1980) argued that hares show presaturation dispersal during phases of population increase and saturation dispersal at peak densities. This hypothesis predicts (*i*) that dispersal rate should be highest in prepeak populations and at intermediate rates of increase (Stenseth 1983) and (*ii*) that animals dispersing during population increase (presaturation types) should be in better condition than animals dispersing at peak populations.

The third hypothesis (Krebs 1978) views dispersal as a selective mechanism whereby rapid-reproducing dispersal types

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leave populations during population increase. At peak densities, most animals in the population are nondispersing types and little dispersal occurs. This hypothesis predicts that (*i*) dispersal rate should be highest during population increase, (*ii*) low in peak populations, and (*iii*) nearly absent in declining populations.

The final hypothesis, proposed by Charnov and Finerty (1980) and developed further by Stenseth (1983), argues that dispersal results from aggressive interactions between unfamiliar individuals. During phases of low density, animals exist in small closely related demes, aggression is low, and few individuals disperse. As density increases, groups become larger, aggression is higher, and more individuals disperse. This hypothesis predicts that dispersal rate should be positively correlated with rate of population increase but not with population density (Stenseth 1983).

We used two methods to monitor dispersal in hares in an attempt to test these four hypothesis. The first was the conventional removal grid method in which animals immigrating to a trapped-out area were operationally defined as dispersers (Myers and Krebs 1971; Gaines and McClenaghan 1980). The second method used radiotelemetry to monitor movements of known individuals.

Study area

Two main areas were used during the study (Fig. 1). There was a control area and a removal area in which all animals captured each session were removed. The location of the removal area was changed (1978 removal to removal; Fig. 1) in 1979, because monitoring of hares in the control area by radiotelemetry suggested that animals had been drawn off the control to the trapped-out area. Both removal areas were trapped intensively to remove the resident population before monitoring of dispersal began. Vegetative cover on the grids was described by Boutin (1983).

Methods

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-door live traps were distributed near alternate stations on runways or in areas of hare cover. They were baited with alfalfa in winter and apples in summer, set for two consecutive nights, and checked each morning. Traps were sometimes set for longer periods on the removal-site if animals still remained on the grid.

Trapping began in 1977 and continued until November 1983. Frequency of trapping varied over the study but was at least once per month and generally more often between February and September. We tried to keep the removal area free of animals which meant that the grid was trapped more often when more animals were caught.

The location, tag number, sex, reproductive condition, weight, length of the right hind foot, and number of wounds were recorded for each capture. Animals were weighed (±5 g) using a Pesola spring scale. Females were scored as lactating if their nipples were large and the surrounding fur was matted. The reproductive condition of males was recorded by determining whether or not their testes were present in scrotal sacs. During June through September, animals captured for the first time were classified as juveniles or adults by visual examination. Juveniles appeared substantially smaller than adults. This technique became less reliable after September when first litter juveniles and adults were similar in size.

Telemetry

Hares caught in the control area and weighing over 700 g were equipped with radio transmitters. We tried to tag all eligible animals, but were unable to do so at peak numbers because of the limited availability of transmitters. Transmitted hares were located by trian-
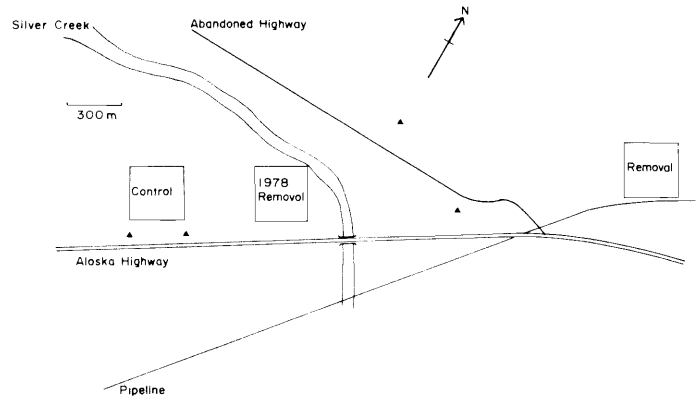

FIG. 1. Location of study areas at Kluane Lake, Yukon (61° N, 138° W). Location of the removal grid was shifted (1978 Removal to Removal) in May 1979. Triangles represent locations of telemetry towers.

gulation from permanent towers near the study areas (Fig. 1; see Boutin 1980 for a full description). The frequency of locations varied but was generally one per day between February 1 and September 30 and between mid- and late-November. At other times, animals were located at least once a week. Animals were checked for activity each time they were located. This was done by holding the receiving antenna stationary and monitoring changes in signal strength. Erratic changes in signal strength indicated that the animal was alive. Animals thought to be dead were tracked with a hand-held antenna until they were sighted. Locations of radios that were considered unusual because of a major change from previous locations were verified by actually locating the radio.

The range of the telemetry system was variable, but radios were regularly detected as far as 5 km from the permanent towers. In spring of each year we tried to locate lost transmitters by monitoring from a high point of land (1700 m) overlooking the study areas. Radios were detected as far as 10 km away. In May 1981, transmitters were searched for by aircraft. To summarize, most transmitters functioning within a 3- to 5-km radius of the control area were detectable from the permanent towers and some radios within a 10-km radius of the control site were detected by special searches. Thus, hares had to disperse at least 5 km and probably further before the transmitter signal was undetectable.

Results

Dispersal and density

Numbers on the control site were estimated by both complete enumeration (Krebs 1966) and Jolly (1965) techniques. Only values from complete enumeration are shown as both techniques showed similar changes. Jolly estimates were about 10% higher on average. Trappability over the entire study was 50.4%. Numbers on the control site were low in 1977 but increased to a peak in fall of 1980 (Fig. 2). In each year, numbers increased between July and October through recruitment of juveniles. In 1978 and 1979, numbers remained constant or declined slightly (1% per week) over winter (November−March). In 1980−1981, however, the rate of overwinter decline was higher (3% per week) until mid-March. Numbers remained stable until mid-May, when the number of males declined by 10% per week for 4 weeks while females increased at a rate of 13% per week. Total numbers again increased in July through juvenile recruitment. After a short decrease the population remained constant until mid-December after which it declined at a rate of 11% per week to early February. Numbers remained constant but low for the duration of the study. On a multiannual basis then, numbers increased
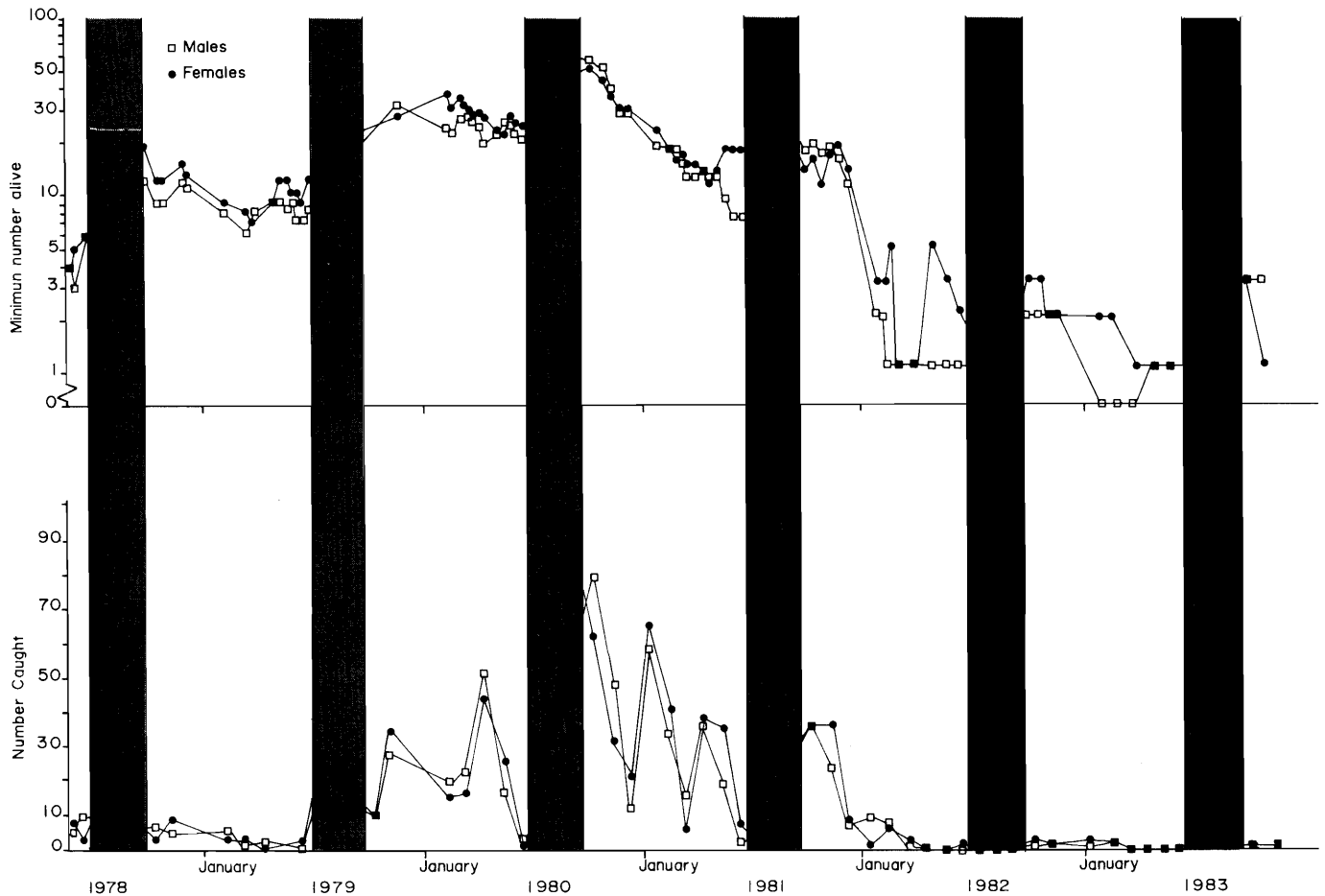
FIG. 2. Minimum number alive on the control site (top) and number of animals caught per month on the removal site (bottom). July through September periods are shaded.

from one year to the next between 1977 and 1980, peaked in 1980, and declined thereafter.

Dispersal, as monitored by the numbers of animals caught on the removal site, occurred throughout the study, but was generally low from July 1978 to July 1979 and from January 1982 to the end of the study (Fig. 2). The highest number of animals was caught on the removal site in September–October 1980; fewer were caught in May–June and relatively more in September–October.

Taking the number of animals caught on the removal site as a measure of the number of dispersers, we defined dispersal rate as the number of hares caught on the removal site at time t divided by population size on the control site at t. We cast the data on dispersal rates into five periods of 2–3 months (Table 1) and determined correlation coefficients between number of dispersers per month, dispersal rate, density on the control site, and rate of population increase (Table 2). The number of immigrants to the removal area was highly positively correlated with density and negatively correlated with rate of population increase. Dispersal rate was not significantly correlated with density but was negatively correlated with rate of population increase. Dispersal rates were highest in December 1980 through April 1981, the time when numbers on the control site began to decline from peak densities (Table 1).

Dispersal as determined by telemetry

Hares with radio collars that were known to have died,

dispersed, or for which radio contact was lost were divided into four categories. (i) Animals that had dispersed: a disperser was defined as any individual which left its initial home range (as determined by the first one to five locations after being collared) to occupy an area distinct (no overlap) from its initial range. (ii) Animals found dead on their home range. (iii) Animals found dead off their home range. (iv) Animals whose fate was unknown (radio transmitter lost). The number of individuals in each category is shown in Table 3. Two hundred and sixty-five different hares were radiocollared. Forty percent of these were less than 1 year old. This value is conservative since only juveniles for which we were sure of age were included. The most striking finding is that of these 265 animals, only 22 (8%) were classed as dispersers. The dispersal rate (column D/A, Table 3) of radiocollared hares was the same during the population increase and peak (mean = 0.05, n = 7) as during the peak and decline (mean = 0.03, n = 11).

Radiocollared dispersers could be missed in two ways. Firstly, contact with radio transmitters could be lost by animals dispersing beyond the range of the telemetry receiver. Most transmitter losses (column E, Table 3) (50%) occurred in the December through February period of 1979–1980 and 1980–1981. This coincides with the time when animals were monitored less intensively, thus increasing the probability of loss. It is doubtful that all transmitter losses could be attributed to dispersal, but the exact proportion is unknown.

A second group of dispersers that may have been missed is

TABLE 1. Changes in population size (minimum number alive, MNA) and rate of increase on the control site during this study. The number of animals caught per month on the removal site and the dispersal rate are also shown

	Average MNA on control site	Rate of increase per individual per year[a]	No. caught on removal site	Dispersal rate
May–June				
1978	9	1.11	8	0.88
1979	19	1.52	15	0.79
1980	48	−0.48	23	0.47
1981	25	−0.88	33	1.31
1982	3	−0.33	1	0.33
1983	2		0	0.00
July–September				
1978	23	0.47	18	0.78
1979	34	1.50	40	1.16
1980	85	−0.48	89	1.05
1981	44	−0.93	41	0.92
1982	3	0.33	1	0.33
1983	4		2	0.50
October–November				
1978	23	1.13	10	0.43
1979	49	0.73	34	0.69
1980	85	−0.62	102	1.19
1981	32	−0.87	36	1.12
1982	4	0.25	5	1.25
1983	5		1	0.20
December–February				
1978–1979	17	1.88	4	0.23
1979–1980	57	−0.28	11	0.19
1980–1981	41	−0.78	97	2.39
1981–1982	9	−0.78	10	1.09
1982–1983	2		2	1.00
March–April				
1979	17	1.94	4	0.24
1980	50	−0.48	66	1.30
1981	26	−0.88	55	2.15
1982	3	−0.33	5	1.41
1983	2		0	0.00

[a]Calculated as $\dfrac{N(t + 1) - N(t)}{N(t)}$.

animals that were found dead off their home range. These may have been killed while dispersing or may have been killed on their home range and carried off by a predator. If hares found off the grid (column C, Table 3) and transmitter losses (column E, Table 3) are classed as dispersers, the maximum proportion of radio collared animals dispersing in any time period was 0.31 (December to February 1979–1980). The average during the population increase was 0.11 ($n = 7$), and it was 0.15 ($n = 11$) during the peak and decline.

To summarize, few radiocollared animals were known to have dispersed at any time during the study. The proportion of radiocollared animals dispersing did not change over the cycle regardless of whether only known dispersers or all potential dispersers were considered.

Population losses and dispersal

In each time period during the study, radiocollared animals were lost from the population. We asked what percentage of these losses could be attributed to dispersal. We provide two values: a minimum that includes only known dispersers and a maximum that includes known dispersers, deaths off the grid,

TABLE 2. Spearman correlation coefficients between measures of dispersal and density and rate of increase of the control site population (minimum number alive, MNA). All values are calculated using 23 samples. Significance levels are shown in parentheses

	Average MNA on control site	Rate of population increase per individual per year[a]
No. caught on the removal site per month	0.85 (0.0001)	−0.60 (0.002)
Dispersal rate	0.14 (0.52)	−0.51 (0.01)

[a]As calculated in Table 1.

and transmitter losses (columns C, D, and E, Table 3). Generally, the average percent losses explained by dispersal was similar during the prepeak (23 minimum, 46 maximum, $n = 7$) and peak (12 minimum, 55 maximum, $n = 5$) periods. Dispersal accounted for an average of 8 (minimum) to 28% (maximum) of the losses occurring during the population decline.

TABLE 3. Fates of hares receiving radio collars during the study. Dispersers were defined as those hares which left their home range (as determined when first tagged) to occupy an area which did not overlap with their initial range. Peak densities on the control site occured in 1980 in each season

		Losses						
	No. of hares with radio collars (A)	Deaths		Dispersers (D)	Transmitters losses (E)	Dispersal rate (D/A)	% losses explained by dispersal	
		On home range (B)	Off home range (C)				Minimum[a]	Maximum[b]
July−September								
1978	26	3	0	3	0	0.11	50	50
1979	29	1	0	0	0	0.0	0	0
1980	64	7	4	2	4	0.03	15	58
1981	47	9	0	1	2	0.02	10	25
October−November								
1978	24	1	1	1	0	0.04	33	66
1979	53	1	2	2	1	0.04	40	83
1980	59	9	5	0	0	0.0	0	35
1981	42	9	1	3	1	0.07	23	35
December−February								
1978−1979	21	5	0	3	3	0.14	38	54
1979−1980	51	6	2	1	13	0.02	11	72
1980−1981	61	23	5	2	6	0.03	7	36
1981−1982	31	16	5	1	0	0.03	5	27
March−April								
1979	18	4	1	0	1	0.0	0	33
1980	33	4	3	2	1	0.06	22	60
1981	30	8	1	0	0	0.0	0	11
May−June								
1979	28	5	1	0	2	0.0	0	37
1980	37	5	1	1	3	0.03	14	50
1981	35	9	4	0	1	0.0	0	35
Totals	265[c]	125	36	22	38			
Average						0.03	15	43

[a]Calculated as D/total losses.

[b]Calculated as $\dfrac{C + D + E}{\text{total losses}}$.

[c]Total number of different animals collared.

TABLE 4. Adults as a proportion of the total number of animals caught on the control and the removal site during July−September. Sample sizes are in parentheses

	Silver Creek	Removal site
1978	0.23 (118)	0.09 (44)
1979	0.35 (95)	0.07 (119)
1980	0.48 (410)	0.06 (278)
1981	0.59 (196)	0.14 (125)

Comparison of dispersers and residents

Sex and age ratios

Sex ratio of animals on the control site was determined by tallying each animal every time it was captured and summing over time periods. Dispersal was not related to sex. Sex ratio on the control site (0.61, $n = 105$) differed from that on the removal site (0.45, $n = 227$) in December to February, 1980−1981 only ($\chi^2 = 7.35$, $P < 0.01$), when more females were caught on the removal site. Animals caught on the removal site were classed as adults or juveniles during the July−September period. We did not distinguish between adults and large juveniles in other periods, so all animals were lumped together. Table 4 shows that dispersal was biased toward juv-

eniles in the July−September period in all years. The proportion of adults was 2.5−8 times higher on the control site than on the removal site. This was probably true during October−November also. Of the radiocollared animals that dispersed, 13 of 22 did so before their first breeding season.

Weight and body size

We next asked whether dispersers and residents differed in body weight (Fig. 3). Adults were excluded from July− September samples because most dispersers were juveniles at this time (at least 86%) while roughly half of the animals caught on the control site were adults (Table 4). We thus tried to eliminate the age differences in the analysis. Both male and female dispersers were lighter than residents during October− November in all years except 1978. This difference between residents and dispersers probably reflects the lack of adults dispersing to the removal site. Male dispersers were also lighter than male residents in May−June 1980 and March−April 1981. Female dispersers were lighter than residents in December−February 1979−1980 and 1980−1981 and May− June 1980. In March−April 1982, female dispersers were heavier than female residents.

We used the length of the right hind foot as a measure of body size. Differences in body size between dispersers and residents followed the same pattern as differences in body
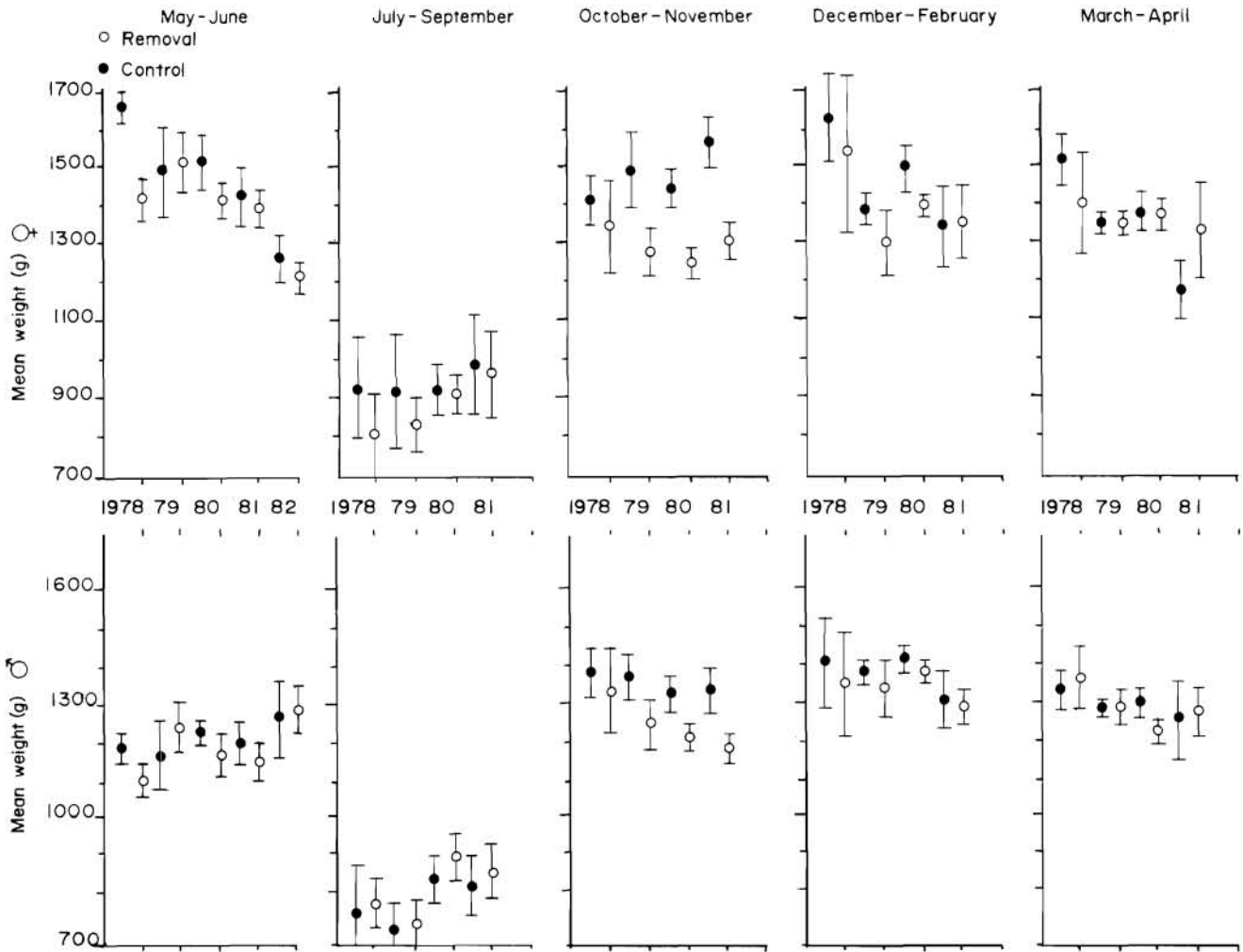
FIG. 3. Mean weights and 95% confidence limits (bars) for male and female hares caught on the control and removal areas. Only juveniles are included in the July−September period.

weight (Fig. 4). Dispersers were smaller on average than residents in October to November. This was true for females in December−February also. Male dispersers were of larger body size than residents in July−September of 1980 and 1981. This was also true of females in 1979.

To summarize, male and female dispersers were smaller and lighter than residents in October−November and in the winter of 1980−1981.

Finally, we asked if dispersers were lighter in body weight during peak and decline phases of the cycle as compared with periods of population increase. Figure 3 shows that there was a tendency for dispersers to be light during the peak and early decline. This was most pronounced in the October−November period. In the July−September period, however, dispersers were actually heavier during the peak and decline than during the increase. It appears then that the average weights of dispersers did not change consistently over the cycle.

Discussion

Most studies of dispersal in small mammals have operationally defined dispersers as animals entering a trapped-out area (Gaines and McClenaghan 1980; Myers and Krebs 1971; Windberg and Keith 1976). The removal grid method may not enumerate dispersers during population declines (Beacham 1980). This study employed radiotelemetry to monitor the

movements of hares that had been trapped on unmanipulated areas. Dispersers were defined as those animals which left their home range to occupy an area that did not overlap with their original home range. This method should detect all types of dispersal (short and long range) and thus preclude the possibility that dispersers were missed during the observed hare decline.

Hare densities in the Kluane Lake area reached peak densities in 1980 and declined to low levels by February 1982. The decline was not caused by high dispersal. Dispersal accounted for a maximum average of 28% of the losses of radiocollared animals during the decline. Most animals died on their home range rather than undergoing dispersal movements (Table 3). Therefore, dispersal was not necessary for the population decline.

Presaturation−saturation hypothesis

Wolff (1980) applied the presaturation−saturation model of dispersal (Lidicker 1975) to snowshoe hares. He argued that hares show presaturation dispersal during periods of population increase and saturation dispersal at peak densities. This model is difficult to test because predictions about dispersal rate relative to rate of population growth and population size are not stated explicitly. Stenseth (1983) argues that the hypothesis predicts that dispersal rate should be (i) positively correlated with population size and (ii) not correlated with rate of popu-
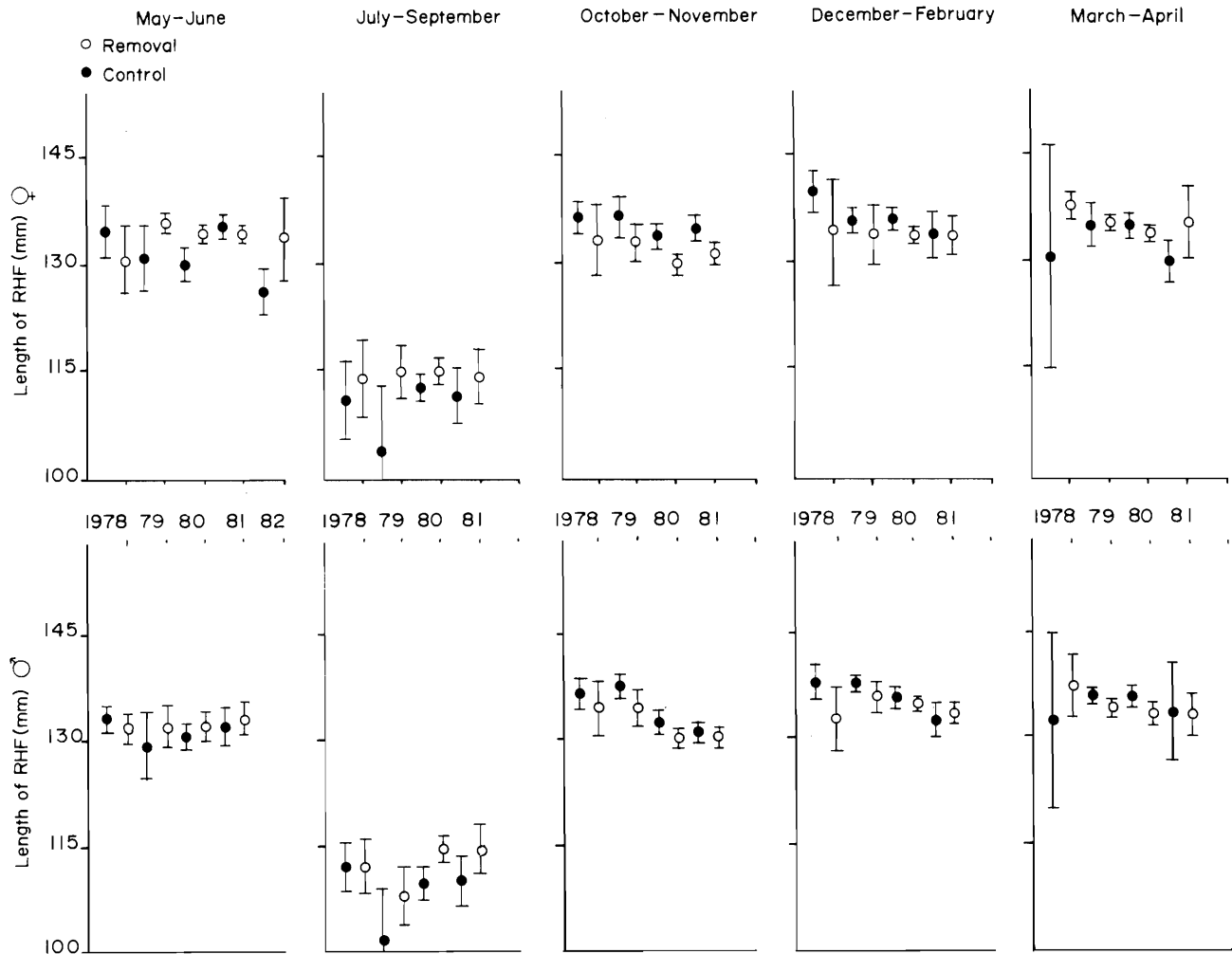
FIG. 4. Mean length and 95% confidence limits (bars) of right hind foot (RHF) as a measure of body size for male and female hares caught on the control and removal areas. Only juveniles are included in the July–September period.

lation increase. We found that dispersal rate, as measured by per capita immigration to the removal grid, was not correlated with density and was negatively correlated with rate of population increase (Table 2). Stenseth (1983) further argues that the presaturation–saturation model predicts that the relationship between dispersal rate and rate of population increase should show a counterclockwise rotation (Fig. 5b) as the population goes from low to increase to peak phases. Similarly, the relationship between dispersal rate and density should show a clockwise rotation. Figure 5e shows that average yearly values obtained in this study followed patterns opposite to those predicted by the presaturation–saturation model.

Finally, the presaturation–saturation model predicts that animals dispersing during phases of population increase (presaturation types) should be in better physical condition than those dispersing at peak and decline densities (saturation types). If body weight is used as a measure of condition, results from this study (Fig. 3) do not support the presaturation–saturation model.

Dispersal and kin-selection hypothesis

A model, proposed by Charnov and Finerty (1980) and expanded by Stenseth (1983), views dispersal as a response to intraspecific aggression which is determined by the degree of relatedness among individuals. During low and early increase phases of population growth, relatedness among individuals is

high, aggression is low, and dispersal is low. As density increases, average relatedness decreases, aggression increases, and dispersal increases. This model predicts (i) a positive correlation between dispersal rate and rate of population increase and (ii) no correlation between density and dispersal rate (Stenseth 1983). It also makes the graphical predictions shown in Fig. 5a. Again results of this study do not support the predictions of the model (Fig. 5e, Table 2).

Selective dispersal hypothesis

Krebs (1978) proposed that dispersal acts as a selective mechanism whereby "dispersal" types leave populations during phases of population increase. At peak densities and during periods of population decline, most remaining members of the population are "nondispersal" types and dispersal rate is low. This hypothesis predicts that dispersal rates should be highest during phases of population increase and low during peak and decline phases (Fig. 5c). Our results indicate that hares were dispersing at a greater rate during the peak and early decline phases than during the period when the population was increasing and thus we reject this model of dispersal.

Food shortage hypothesis

Windberg and Keith (1976) recorded the number of hares that dispersed to a removal area during a population peak and decline. They found the highest dispersal rate during the winter

of peak densities. Dispersers were also lighter than residents at this time. They argued that this, along with a higher incidence of scarring in dispersers versus residents, reflected the intra-specific competition for food in control populations. We found that dispersal rates during seasons when hares were feeding on woody browse (October through April) showed pronounced increases, beginning in the year of peak densities (1980). This was particularly true in December through February and March through April (Table 1), when food shortage is likely to be most acute. We also found that lighter and smaller hares were dispersing at this time (Figs. 3 and 4). Scarring of animals was low throughout the study (18 cases on the removal site, 11 cases on the control site) and not concentrated in any season or time period. Our results are consistent with the hypothesis that increased dispersal of hares during peak and declining densities is a response to food shortage (Figs. 5*d* and 5*e*).

Examination of other studies

After reviewing dispersal studies of cricetid rodents. Gaines and McClenaghan (1980) concluded that in most cases, dispersal rate was higher in increasing populations and thus supported the selective dispersal hypothesis. They used the percentage of losses (number of tagged animals disappearing from a control area) owing to dispersal (number of tagged animals appearing on a removal grid) as a measure of dispersal rate. However, the percent losses as a result of dispersal are not a measure of dispersal rate because the proportion of animals lost from the population varies with phase of the cycle, being higher during periods of decline. As a result, dispersal may explain a lower percentage of losses at this time but the proportion of the total population lost through dispersal is unchanged. Krebs et al. (1976) found that per capita dispersal rate of voles was correlated with rate of population increase, which they interpreted as meaning more animals were dispersing when the population was increasing than while declining. However, their results may reflect a seasonal rather than multiannual effect. More animals dispersed during breeding seasons which coincided with periods of high increase. Beacham (1980) was able to separate seasonal from multiannual effects and found no difference in the number of dispersers leaving increasing versus declining populations. He found more animals dispersing at high than at low density, as was the case in this study.

Windberg and Keith (1976) suggested that dispersers at peak densities suffered higher mortality rates than residents. They do not state explicitly whether they consider dispersal necessary for declines in hare numbers but if the above is true, dispersal would at least increase the rate of decline. Results from monitoring of radiocollared animals in this study indicated that dispersal was unimportant during the decline. Most animals died on their home range and dispersal movements were not required to increase the probability of mortality.

Methods of studying dispersal

Both the removal grid and telemetry techniques of monitoring dispersal sample only those animals that are trappable. Most juvenile hares do not reach a trappable size until they are at least 4 weeks old and they were not radiocollared for another 3−4 weeks. Other work indicates that hares do undergo dispersal movements at an early age (Boutin 1984*a*). As a result, the above methods probably underestimate dispersal during the summer months. At other times of the year, all animals were large enough to be trapped and collared.

The amount of dispersal measured by the removal grid technique differed from that determined by telemetry in two ways.
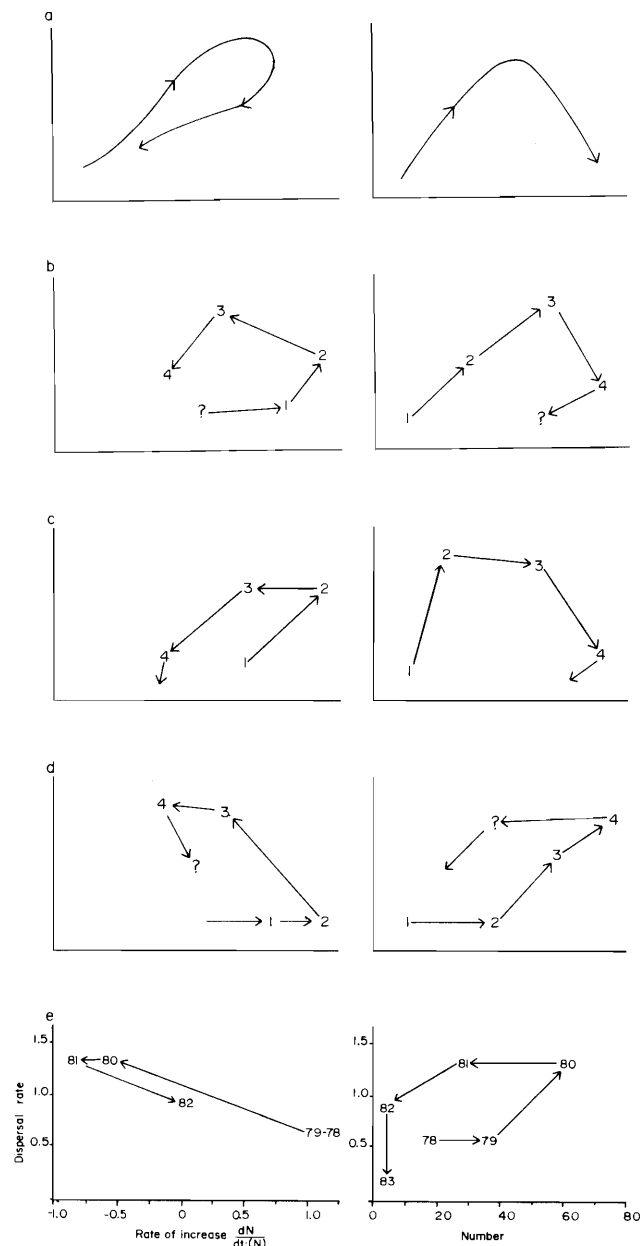

FIG. 5. Relation between changes in dispersal rate and rate of increase (left) and numbers (right): (*a*) as predicted by the dispersal kin selection hypothesis (redrawn from Stenseth 1983); (*b*) as predicted by the presaturation−saturation hypothesis (redrawn from Stenseth 1983); (*c*) as predicted by the selective dispersal hypothesis; (*d*) as predicted by the food shortage hypothesis (numbers represent stages of population growth with 1 being the bottom phase and 4 the peak phase); and (*e*) actual average values obtained from this study (numbers represent years with 1980 being the year of peak density).

First, the large number of immigrants appearing on the removal grid suggested that dispersal was prominent while telemetry indicated that few animals dispersed at any time during the study. Second, the per capita rate of dispersal, as measured by the removal grid, indicated that dispersal was highest in peak and early decline phases of the cycle. However, the proportion of radiocollared hares that dispersed did not change with phase of the cycle. Why did results from the two methods differ?

Animals that immigrated to the removal grid could have come from as far away as 5 km or greater. Source populations then cover an area many times greater than the area covered by

the control grid. Consequently, the large number of animals caught on the removal site may constitute a very small proportion of the surrounding population. Actual dispersal rate (dispersers per individual) is probably very low and the measure we use as dispersal rate is merely an index that can reflect changes but not absolute rates. Dispersal rates determined by telemetry are probably a better measure of the proportion of animals actually dispersing.

The use of a removal grid as an experimental method to monitor dispersal assumes that the removal area does not affect animals on the control area and that the animals being removed are actual dispersers as opposed to individuals making brief forays from their home range (Krebs et al. 1976). The location of the removal grid was moved in this study because radiotelemetry suggested that movements of animals on the control site were affected by the presence of the removal site. After relocation of the removal site in 1979, only nine tagged individuals from the control site were captured there. Given random direction of dispersal, the proportion of tagged dispersers encountering a removal area is highly dependent on its distance from the control area; an expected maximum would be 25%.

Our use of telemetry to monitor dispersal recorded virtually all losses owing to dispersal. Yet the percentage of losses explained by dispersal in this study was lower than most studies using recovery of tagged individuals on a removal area (Gaines and McClenaghan 1980). This means that dispersal was either much less common in snowshoe hares than in other species of small mammals, or that removal grid studies overestimate losses owing to dispersal, possibly because they are too close to the control area. Animals may be attracted to the removal area because of the reduced density there. Tamarin (1978) provides evidence that more tagged voles were caught on a removal grid used in his study than was expected by random movement. Dobson (1981) argued that an abnormal sex ratio of ground squirrels on a control area was due to dispersal of animals to a nearby removal area.

The removal of animals from an area also alters its favorability relative to that of surrounding areas. The relative difference in density between that on the removal area and that in surrounding areas will change over a population cycle. During the increase phase of the cycle, the removal grid may merely represent one patch among many which is free of hares. As numbers build, however, and more habitats become occupied, the removal grid will become more favorable and thus overestimate the average amount of dispersal that is occurring. Also, if hares encounter winter food shortage during peak populations, the removal grid may have relatively more food because density and browsing pressure are lower. The removal area then attracts hares and would do so more strongly during peak densities. This explains why there was an increase in per capita dispersal as measured by the removal grid but no increase as measured by telemetry.

How can the removal area "attract" animals? It is possible that hares make forays off of their home ranges to assess the favorability of surrounding areas. We recorded five instances in which radiocollared animals made long-range movements off their home ranges for 1 to 2 days and then returned. Whether an animal actually becomes a disperser (leaves its home range permanently), is probably dependent on conditions in surrounding areas as well as in its home area. A removal grid may overestimate dispersal by preventing animals that would normally return to their home range from doing so (caught in traps) or by having them remain on the grid because conditions

are unusually favorable. This is more likely to occur during periods of high density when animals would not normally find vacant areas to settle and so return to their original home range. If this situation occurs, the removal grid violates the assumption that it is sampling true dispersers rather than individuals making brief forays off their home ranges. These animals are potential dispersers but the availability of vacant habitat dictates whether they actually become dispersers.

The attraction of hares to the removal grid during the peak and early decline phases of the cycle is further support for the hypothesis that food shortage was responsible for the increase in dispersal. We obtained similar increases in immigration in spring of 1981 on an experimental grid that received supplemental food (Boutin 1984b). Animals appeared to be searching for and occupying areas of favorable food supply.

To conclude, results of this study are consistent with the hypothesis that dispersal of hares, particularly in winters of peak and declining populations, is due to food shortage. However, dispersal was not necessary to explain the observed population decline. During the decline most animals died on their home ranges.

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