NATAL DISPERSAL OF SNOWSHOE HARES DURING A CYCLIC POPULATION INCREASE

ELIZABETH A. GILLIS AND CHARLES J. KREBS

Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, British Columbia, Canada V6T 1Z4

We used radiotelemetry to monitor movements of 35 juvenile snowshoe hares (*Lepus americanus*) from weaning until their first breeding season (June 1995–April 1996). Juveniles born on control or food-addition areas were assigned to one of three cohorts of litters. We calculated natal dispersal distances (distance from nest site to breeding location) and frequencies of emigration (proportion dispersing more than twice the home-range diameter of adults) and determined ages and dates at emigration. Natal dispersal distances ranged from 23 m to >16 km. Fifty percent (9/18) of juveniles that survived until their first breeding season emigrated. Juveniles from the third litter dispersed at an older age than those from first or second litters. We detected no statistically significant effect of food addition on dispersal distance. With our small sample, we did not find statistical evidence of sex-biased natal dispersal (7 of 12 males and 2 of 6 females dispersed).

Key words: *Lepus americanus,* snowshoe hare, natal dispersal, food addition, population cycles, Yukon

Dispersal can affect population dynamics by influencing genetic and demographic structure and by establishing new populations (Gaines and McClenaghan, 1980; Stenseth and Lidicker, 1992). Dispersal also may be a necessary component in the regulation of some populations that cycle (Gaines et al., 1979; Krebs et al., 1973) and prevent populations from cycling in some locations (Buehler and Keith, 1982; Dolbeer and Clark, 1975).

For snowshoe hares (*Lepus americanus*), which undergo a 9–11-year population cycle throughout much of their range, dispersal appears to be highest during winters of peak and early decline (Boutin et al., 1985; Windberg and Keith, 1976), although dispersal is not necessary for the population to decline (Boutin et al., 1985). Juveniles are the predominant dispersers in hares, and many researchers have stressed the importance of studying natal dispersal at all stages of the hare cycle (Keith, 1981, 1990; O'Donoghue and Bergman, 1992). Juvenile hares can disperse shortly after weaning (24–28 days old—Boutin, 1984; O'Donoghue and Bergman, 1992) or at any time of the year (Boutin, 1979; Keith et al., 1984, 1993), and can disperse large distances (20 km reported by O'Farrell, 1965), moving up to 700 m in 1 night (O'Donoghue and Bergman, 1992). However, it is not known what factors affect natal dispersal in hares. Hares also are multi-littered synchronous breeders (Cary and Keith, 1979), and it is not known if natal dispersal distances or frequencies differ among cohorts of litters born during the summer.

Our goal was to obtain information on natal dispersal of snowshoe hares via radiotelemetry during the increase phase of a population cycle of snowshoe hares. To determine which factors may influence dispersal in juvenile hares, we studied males and females from three cohorts of litters born in 1995 on food-addition and control areas. Food addition areas had been supplemented with commercial rabbit chow since 1986 (Hodges et al., in press *b*). Specifically, our objectives were to quantify natal dispersal distances, ages at emigration, and probability that a juvenile would emigrate, and to determine if these measures differed among cohorts of litters and between males and females in areas with supplemental food compared with control areas.

MATERIALS AND METHODS

Our study was carried out from June 1995 to April 1996 in conjunction with the Kluane Boreal Forest Ecosystem Project near Kluane Lake, Yukon Territory, Canada (60°57′N, 138°12′W). Vegetation in the study area was predominantly forest of white spruce (*Picea glauca*), with an understory of willow (*Salix*), bog birch (*Betula glandulosa*), and soapberry (*Sherpherdia canadensis*—Boutin et al., 1995; Douglas, 1974). We studied hares on five areas, three control areas (two 36-ha grids and one off-grid site) and two 36-ha food-addition grids. On food-addition grids, commercial rabbit chow (minimum 16% crude protein) was spread evenly every 5–10 days along four equally spaced lines running the length of the grids (Hodges et al., in press *b*).

Various terms have been used by different authors in the literature on dispersal. The definitions we used were as follows. Natal dispersal was the movement the animal made from its birthplace to the place where it reproduced or would have reproduced if it survived and found a mate (Howard, 1960). Natal dispersal distance was the linear distance from an individual's nest site to its breeding location. An emigrant was a hare with a dispersal distance >twice the home-range diameter of adults (>812 m for males, >554 m for females—K.E. Hodges pers. comm.). That distance was used to distinguish home ranges that potentially overlapped with the natal home range from those that did not. To be classified as an emigrant, the hare could not return to its natal area before it died or ≤1 month. Emigration distance was the distance moved by hares classified as emigrants; emigration distances were a subset of dispersal distances. A philopatric hare was a hare that was not classified as an emigrant (i.e., dispersed <twice the home range-diameter of adults). Sex-biased dispersal was the differences in dispersal distance, proportion of emigrants, or timing of emigration between sexes.

Trapping for juvenile hares began on all study sites in June 1995 when juveniles from the first litters were ca. 4–5 weeks old and continued throughout summer and early autumn to capture juvenile from second and third litters. Eighty-six Tomahawk traps (Tomahawk Live Trap Company, Tomahawk, WI) were set among eight rows of each grid being trapped. All grids were trapped 2–6 nights in October 1995 and March 1996 as part of the annual censusing protocol carried out by the Kluane Boreal Forest Ecosystem Project (Boutin et al., 1995).

Hares were eartagged with numbered No. 3 Monel tags (National Band and Tag Company, Newport, KY) when first captured, and at every capture, the hare's tag, trap location, weight, length of right-hind foot, sex, reproductive condition, and age (adult or juvenile) were recorded. Hares were identified as juveniles based on weight, right-hind foot length, and, if male, penis shape (Keith et al., 1968). We assigned juveniles to a litter cohort (1–3) based on weight and right-hind foot length, using measurements of juveniles from known litter cohorts as a guide.

We collared juvenile hares with radiocollars (TW-3 transmitters—Biotrack Ltd., Dorset, United Kingdom) that we had padded with 1.5 cm of foam to allow for growth. Weight of collars never exceeded 5% of the hare's body weight.

Locations of nests were determined two ways. Twenty-five of the 35 hares used in our study were tagged at birth, and for those hares, an exact nest site location was known (Stefan, 1998). For other hares, we used the site at which the juvenile was first captured as the nest site if it was trapped at <35 days old, because previous studies indicated that few hares dispersed younger than that age (O'Donoghue and Bergman, 1992). We did not determine nest sites for hares that were captured first at >35 days of age. We determined the hare's age at first capture using the mean date of birth for each litter cohort on each grid because parturition dates of females within local areas were synchronous (Stefan, 1998). A fourth cohort of litters was born in 1995, but we did not include those hares in the analysis because the parturition date for that cohort was not known accurately.

Locations of hares were obtained by telemetry and trapping. From July to October 1995, and again during February and March 1996, individual hares were tracked and visually located. Each grid contained 400 permanent stakes in a 20 by 20 grid system with 30 m between stations, and the hare's location relative to those stakes was recorded for animals located on grids (accurate to 5 m). For animals located off the permanent grid systems, we recorded locations via a global positioning system (GPS—Trimble Navigation Limited, Sunnyvale, CA) that was accurate to 10–30 m. Locations of depredated hares were included in the analysis only if we were confident the location of remains was close to the location of the kill. Locations of hares trapped on grids were recorded as location of the nearest grid stake and positions of traps at the offgrid site were determined using GPS. All locations were converted to Universal Transverse Mercator (UTM) coordinates to facilitate calculation of linear distances moved.

Natal dispersal distances were calculated as the linear distance from the nest site to the animal's location in the spring. For each hare, we averaged all locations obtained in February–March to obtain one location for spring. Animals that did not survive until February 1996 (1 month before the breeding season) were eliminated from the analysis because we could not be certain of where they would have bred if they had survived.

To determine date and age at which juveniles emigrated, we calculated the linear distance of the hare's location to its nest site each time a radiocollared juvenile was located (2–34 times/individual, $\bar{X} = 12$). We then established the earliest and latest possible dates at which an individual hare first moved more than twice the home-range diameter of adults from its nest site. We classified that movement as a foray if the hare returned to within two home-range diameters of the nest site in <1 week and as emigration if the hare remained more than two home-range diameters from the nest site for >1 month. Median date between the earliest possible and latest possible date was used in the analysis if the difference between the two was <1 week. Hares were excluded from the analysis if the difference was >1 week because the true date was too uncertain. We converted dates of emigration to ages at emigration by subtracting mean date of birth for each litter cohort on each grid from the date of emigration. All animals that emigrated were included in this analysis, even if they did not survive until spring.

We compared dispersal distances among cohorts with Kruskal-Wallis tests. We compared dispersal distances between sex and treatments (control versus food addition) with logistic regression, which allowed us to treat dispersal distance as a continuous variable while treating either sex or food treatment as categories (Trexler and Travis, 1993). Data on age at emigration were analyzed by an analysis of variance (ANOVA) with log age of emigration as the dependent variable. Because of small samples, we examined only main effects (litter, sex, treatment). We used the product-moment correlation coefficient to evaluate relationships between age and date of emigration and emigration distance. We performed logistic regressions with JMP (SAS Institute, Inc., 1994) and all other statistical analyses on SYSTAT (SPSS Inc., 1997). For all tests, we used $P < 0.10$ as the level of statistical significance.

RESULTS

Population densities of hares on food-addition and control areas changed in a cyclic manner with a population increase, peak, and decline from 1987 to 1993 (Krebs et al., 1995). Our study took place during the early increase phase of the hare cycle (1995–1996—Hodges et al., in press *a*). Densities of hares on the food-addition grids ranged from 2.5 to 3.1 times that on control grids during our study.

Natal dispersal.—Eighty-four juvenile snowshoe hares were radiocollared. We were able to determine locations of nest sites for 35 of those hares, 18 of which survived until February 1996. Fifty percent of all collared hares that could be used to study natal dispersal (18/35) and those that survived until spring (9/18) emigrated (Table 1). Among hares that survived until spring, natal dispersal distances ranged from 23 m to >16 km (Fig. 1). Natal dispersal distances did not differ among cohorts of litters ($\chi^2 = 0.46$, *d.f.* $= 2$, $P = 0.80$) so litter cohorts were combined for analyses of natal dispersal. No relationship was found between treatment (hares born on food-addition versus control areas) and dispersal distance ($\chi^2 = 0.74$, *d.f.* $= 1$, $P = 0.39$) so hares from both food-addition and control areas were pooled to test for sex-biased dispersal. No relationship was found

TABLE 1.—*Proportions of juvenile hares that emigrated from their natal home range before their first breeding season; only hares that survived from their birth in summer 1995 until their first breeding season (spring 1996) are included.*

Category	*n*	Number of emigrants	Proportion of individuals that emigrated
All juveniles	18	9	0.50
Control			
Male	8	4	0.50
Female	4	2	0.50
Food-addition			
Male	4	3	0.75
Female	2	0	0.00
Litter 1			
Male	5	4	0.80
Female	1	0	0.00
Litter 2			
Male	5	2	0.40
Female	2	1	0.50
Litter 3			
Male	2	1	0.50
Female	3	1	0.33

between sex and dispersal distance ($\chi^2 = 0.56$, $d.f. = 1$, $P = 0.45$).

Timing of emigration and foray activity.—Of the 18 juveniles that emigrated, dates of emigration could be established for 15 hares, 14 of which had known dispersal distances. Juveniles from the third cohort of litters emigrated at an older mean age (84 days old) than juveniles from litters 1 and 2 (48 and 42 days respectively), but neither food addition nor sex significantly affected age of emigration (food addition, $F = 0.001$; $d.f. = 1, 10$; $P = 0.97$; sex, $F = 2.17$; $d.f. = 1, 10$; $P = 0.17$; litter, $F = 6.24$; $d.f. = 2, 10$; $P = 0.02$; Fig. 2). A significant positive correlation existed between emigration distance and age at emigration ($r^2 = 0.37$, $d.f. = 12$, $P = 0.02$) when two apparent outliers were included (without outliers, $r^2 = 0.00$, $d.f. = 10$, $P = 0.97$, Fig. 3a). Emigration distance and date of emigration were not significantly correlated unless an outlier was removed from the analysis (with outlier: $r^2 = 0.01$, $d.f. = 12$, $P = 0.97$, without outlier: $r^2 = 0.24$, $d.f. = 11$, $P = 0.09$, Fig. 3b). For age at emigration and date of emigration, the relationship with emigration distance depend-

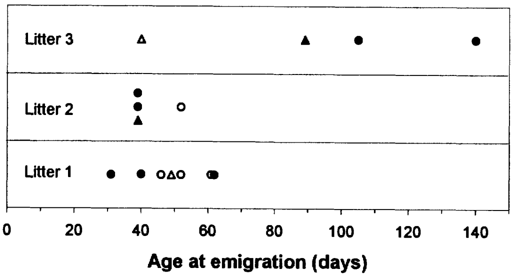

FIG. 2.—Ages at which juvenile snowshoe hares emigrated. Closed symbols represent hares born on control areas, open symbols represent hares born on food-addition areas, circles represent males, and triangles represent females. Only hares whose ages at emigration were known to within 1 week are included in the analysis ($n = 15$).

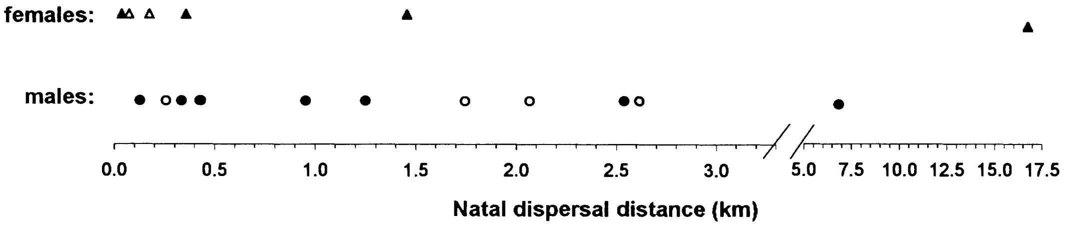

FIG. 1.—Natal dispersal distances for juvenile hares born in 1995 that survived until their first breeding season in 1996 ($n = 18$). Closed symbols represent hares born on control areas and open symbols represent those born on food-addition areas. Two symbols representing males on control areas overlap at 0.42 and 0.43 km.

ed on one or two points; over the majority of ages and dates, no relationship was detected.

Some hares exhibited exploratory movements before dispersing. Forays were observed in three hares, two males which emigrated 2 and 10 days after the foray had been made, and one female, which did not emigrate. Another individual dispersed ca. 900 m from his nest site at 62 days of age but returned to his natal area between 65 and 203 days later.

DISCUSSION

In our study, natal dispersal distance of snowshoe hares ranged from 23 m to >16 km, with 50% of juvenile hares emigrating (9 of 18). The dispersal distance of 16 km reported here is the second largest value reported for snowshoe hares in an unmanipulated population. O'Farrell (1965) reported that a female snowshoe hare was killed 20 km from her original trap location. A dispersal distance of 33 km has been documented for the Arctic hare (*Lepus timidus*—Marcström et al., 1989). Whether or not these large distance dispersal distances in hares are atypical is unknown because prior studies relying on trapping may have failed to detect long distance dispersers (Koenig et al., 1996).

Frequency of emigration in our study was higher than that found by other researchers. Boutin et al. (1985) reported a maximum loss due to dispersal of 28% during the decline phase of the hare cycle (*n* = 265), and Keith et al. (1993) reported that only 2.5% (5/194) of hares dispersed in a noncyclic population in Wisconsin. However, most previous studies have not separated juveniles and adults when calculating dispersal frequency. Because juveniles are the predominant dispersers in hares (Boutin et al., 1985; Keith, 1990; Keith et al., 1984; Windberg and Keith, 1976), earlier estimates probably underestimate emigration by juveniles. In a study conducted during the increase phase of another hare cycle in the same area as our study, 28% of juvenile hares (9 of 32 individuals with radiocollars) dispersed between August 14 and the following March 31 (Boutin, 1979). Because that estimate included 12 animals that died on the study grids before their first breeding season, it was probably low. If only individuals that survived to spring are considered, 45% (9 of 20) of juvenile hares dispersed in the study by Boutin (1979). In addition, 70% of juveniles trapped in November were classified as immigrants in each of 2 years of peak densities of hares (Boutin, 1984), suggesting dispersal rates may be higher during the peak of the hare cycle.

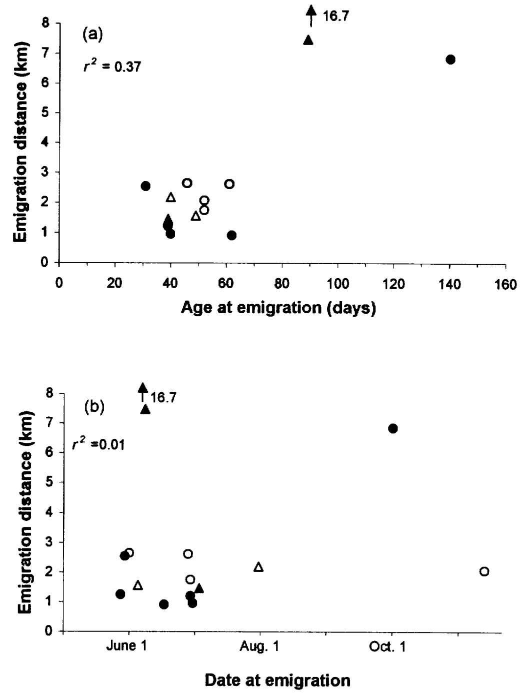

FIG. 3.—Relationship between emigration distance and a) age of emigration and b) date of emigration for hares. Closed symbols represent hares born on control areas, open symbols represent hares born on food-addition areas, circles represent males, and triangles represent females. Two symbols representing males on control areas overlap at 39 days, 0.12 km in (a). Only hares whose ages at emigration were known to within 1 week and whose dispersal distance were known were included in the analysis (*n* = 14).

We detected no effect of food addition on either dispersal distance or proportion of juveniles that emigrated. We predicted decreased dispersal on food-addition areas if limited availability of food was a proximate cause of dispersal and increased dispersal if density was a proximate cause of dispersal. It seems unlikely that food or density by themselves influenced dispersal in juvenile hares, but we cannot determine if food and density together influenced dispersal.

Male-biased natal dispersal is common for most species of mammals (Dobson, 1982; Greenwood, 1980). In our study, dispersal distances, emigration frequencies, and age at emigration did not differ between males and females, but samples are small. Other studies of snowshoe hares also have not detected sex-biased dispersal (Boutin, 1979, 1984; Windberg and Keith, 1976). An exception is the study by O'Donoghue and Bergman (1992), in which male-biased dispersal, defined by the timing of dispersal and proportion of each sex which bred on their natal grid the following year, was reported during the peak of the hare cycle.

Individuals from first and second litters emigrated at a younger age than individuals from third litters. Females may nurse their last litter of the season longer (O'Donoghue and Bergman, 1992), and because not all females produced a fourth litter, some individuals from third litters may have been weaned at an older age than individuals from first and second litters. However, our finding is based on a very small number of third-cohort juveniles (three of four showed late dispersal), and therefore any conclusions should be considered tentative. Other studies of snowshoe hares have reported juveniles from first and second litters emigrating throughout winter (Boutin, 1979; Keith et al., 1984, 1993; Windberg and Keith, 1976). In contrast, only one of eight juveniles from first litter emigrated in winter in our study. All other juveniles emigrated before November.

A positive correlation between age at emigration and emigration distance was expected because individuals that disperse at a younger age may have a better chance of finding and becoming established in vacant areas closer to their natal home range (Waser, 1985). Snowshoe hares are not territorial, but they do exhibit spacing behavior (Boutin, 1980, 1984) and emigrating snowshoe hares that arrive later in the season may have more difficulty becoming established as residents (Boutin, 1984; Graf and Sinclair, 1987). Although we found a significant positive correlation between age at emigration and emigration distance, those findings depended upon a few outliers (Fig. 3). In the range of ages over which most hares emigrated (30–60 days), there was no relationship between age at emigration and distance of dispersal. We therefore classify this relationship, and the similar relationship between date of emigration and emigration distance, as biologically nonsignificant.

Our study reports the first baseline information on natal dispersal of snowshoe hares from data gathered by telemetry. Although it was previously known that juveniles disperse more often than adults (Boutin et al., 1985; Keith et al., 1984; Windberg and Keith, 1976), the emigration frequency of 50% that we found was the highest value reported for snowshoe hares. This high emigration rate suggests that natal dispersal may play a larger role in the population dynamics of snowshoe hares than previously thought.

ACKNOWLEDGMENTS

T. K. Y. Chu, J. DeGroot, and J. Jakeilek assisted with the field work and J. H. Myers, L. Gass, A. R. E. Sinclair, C. Stefan, K. Hodges, A. Byrom, J. Ruesink, and two anonymous reviewers provided valuable comments on the manuscript. The facilities for this study, the Kluane Lake Research Station, were maintained by the Arctic Institute of North America. Funding for this study was provided by the Natural Sciences and Engineering Research Council (NSERC) of Canada to C. J. Krebs and a Northern Scientific Training Program grant to E. Gillis. E. Gillis was supported by a PGS-A award from NSERC. This publication is #118 of the Kluane Boreal Forest Ecosystem Project.

LITERATURE CITED

BOUTIN, S. 1980. Effect of spring removal experiments on the spacing behavior of female snowshoe hares. Canadian Journal of Zoology, 58:2167–2174.

BOUTIN, S. A. 1979. Spacing behavior of snowshoe hares in relation to their population dynamics. M.Sc. thesis, University of British Columbia, Vancouver.

———. 1984. The effect of conspecifics on juvenile survival and recruitment of snowshoe hares. The Journal of Animal Ecology, 53:623–637.

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. Canadian Journal of Zoology, 63:106–115.

BOUTIN, S., ET AL. 1995. Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. Oikos, 74:69–80.

BUEHLER, D. A., AND L. B. KEITH. 1982. Snowshoe hare distribution and habitat use in Wisconsin. The Canadian Field-Naturalist, 96:19–29.

CARY, J. R., AND L. B. KEITH. 1979. Reproductive changes in the 10-year cycle of snowshoe hares. Canadian Journal of Zoology, 57:375–390.

DOBSON, F. S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. Animal Behaviour, 30:1183–1192.

DOLBEER, R. A., AND W. R. CLARK. 1975. Population ecology of snowshoe hares in the central Rocky Mountains. The Journal of Wildlife Management, 39:535–549.

DOUGLAS, G. W. 1974. Montane zone vegetation of the Alsek River region, south-western Yukon. Canadian Journal of Botany, 52:1016–1033.

GAINES, M. S., AND L. R. MCCLENAGHAN, JR. 1980. Dispersal in small mammals. Annual Review of Ecology and Systematics, 11:163–196.

GAINES, M. S., A. M. VIVAS, AND C. L. BAKER. 1979. An experimental analysis of dispersal in fluctuating vole populations: demographic parameters. Ecology, 60:814–828.

GRAF, R. P., AND A. R. E. SINCLAIR. 1987. Parental care and adult aggression toward juvenile snowshoe hares. Arctic, 40:175–178.

GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour, 28:1140–1162.

HODGES, K. E., C. J. KREBS, AND A. R. E. SINCLAIR. In press *a*. Snowshoe hare demography during a cyclic population low. The Journal of Animal Ecology.

HODGES, K. E., C. I. STEFAN, AND E. A. GILLIS. In press *b*. Does body condition affect fecundity in a cyclic population of snowshoe hares? Canadian Journal of Zoology.

HOWARD, W. E. 1960. Innate and environmental dispersal of individual vertebrates. The American Midland Naturalist, 63:152–161.

KEITH, L. B. 1981. Population dynamics of hares. Pp. 395–440, *in* Proceedings of the world lagomorph conference (K. Myers and C. D. MacInnes, eds.). University of Guelph, Guelph, Ontario, Canada.

———. 1990. Dynamics of snowshoe hare populations. Pp. 119–195, *in* Current mammalogy (H. H. Genoways, ed.). Plenum Press, New York.

KEITH, L. B., S. E. M. BLOOMER, AND T. WILLEBRAND. 1993. Dynamics of a snowshoe hare population in fragmented habitat. Canadian Journal of Zoology, 71:1385–1392.

KEITH, L. B., E. C. MESLOW, AND O. J. RONGSTAD. 1968. Techniques for snowshoe hare population studies. The Journal of Wildlife Management, 32: 801–812.

KEITH, L. B., J. R. CARY, O. J. RONGSTAD, AND M. C. BRITTINGHAM. 1984. Demography and ecology of a declining snowshoe hare population. Wildlife Monographs, 90:1–43.

KOENIG, W. D., D. VAN VUREN, AND P. N. HOOGE. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. Trends in Ecology and Evolution, 11:514–517.

KREBS, C. J., M. S. GAINES, B. L. KELLER, J. H. MYERS, AND R. H. TAMARIN. 1973. Population cycles in small rodents. Science, 179:35–41.

KREBS, C. J., ET AL. 1995. Impact of food and predation on the snowshoe hare cycle. Science, 269:1112–1115.

MARCSTRÖM, V., L. B. KEITH, E. ENGREN, AND J. R. CARY. 1989. Demographic response of arctic hare (*Lepus timidus*) to experimental reductions of red foxes (*Vulpes vulpes*) and martens (*Martes martes*). Canadian Journal of Zoology, 67:658–668.

O'DONOGHUE, M., AND C. M. BERGMAN. 1992. Early movements and dispersal of juvenile snowshoe hares. Canadian Journal of Zoology, 70:1787–1791.

O'FARRELL, T. P. 1965. Home range and ecology of snowshoe hares in interior Alaska. Journal of Mammalogy, 46:406–418.

SAS INSTITUTE, INC. 1994. JMP statistical software for the Macintosh. SAS Institute, Inc., Cary, North Carolina.

SPSS INC. 1997. SYSTAT 7.01 for Windows. SPSS Inc., Chicago, Illinois.

STEFAN, C. I. 1998. Reproduction and pre-weaning juvenile survival in a cyclic population of snowshoe hares. M.S. thesis, University of British Columbia, Vancouver, Canada.

STENSETH, N. C., AND W. Z. LIDICKER, JR., (EDS.). 1992. Animal dispersal: small mammals as a model. Chapman and Hall, New York.

TREXLER, J. C., AND J. TRAVIS. 1993. Nontraditional regression analyses. Ecology, 74:1629–1637.

WASER, P. M. 1985. Does competition drive dispersal? Ecology, 66:1170–1175.

WINDBERG, L. A., AND L. B. KEITH. 1976. Experimental analyses of dispersal in snowshoe hare populations. Canadian Journal of Zoology, 54:2061–2081.

Submitted 20 April 1998. Accepted 13 November 1998.

Associate editor was Edward J. Heske.