

**NATAL DISPERSAL AND POST-WEANING SURVIVAL OF JUVENILE
SNOWSHOE HARES DURING A CYCLIC POPULATION INCREASE**

by

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ABSTRACT

Juvenile snowshoe hares (*Lepus americanus*) in southwestern Yukon were monitored using radio telemetry to determine the effects of litter group on natal dispersal and post-weaning survival. A total of 84 juveniles representing the four litter groups born in 1995 were monitored from June 1995 to April 1996 on control areas and areas in which supplemental food was provided. Natal dispersal distance, age and date of emigration, survival rate, and proximate cause of death were examined.

Natal dispersal distances (distance from nest site to site of first breeding) of hares ranged from 23 m to over 16 km. Fifty percent (9/18) of juveniles whose nest sites were known and survived until their first breeding season were classified as emigrants (dispersed a distance further than two adult home range diameters). Emigrants did not suffer significantly higher mortality than those individuals which did not emigrate. Neither dispersal distance nor the proportion of hares which emigrated differed between food addition and control areas. On the control areas, there was no evidence of sex-biased natal dispersal. However, on the food addition areas, a higher proportion of males than females emigrated and males dispersed significantly farther than females. This pattern possibly resulted from the increased population density on the food addition areas.

Age at emigration varied from 31 days to 140 days, but was not related to the sex of the individuals. Food addition had no observable effect on emigration age, however there was a significant effect of litter group. Third litter juveniles emigrated at an older mean age (84 days) than first (48 days) and second (42 days) litter juveniles.

Twenty-eight day survival did not differ between food addition and control areas for any litter group. Over the study period, 28-day survival of juveniles (all litters combined) did not differ significantly from adults (juveniles: 0.91, adults: 0.93). However, when examined by litter group, third litter survival was significantly lower than adult and second litter survival, while fourth litter survival was significantly lower than adult, first, and second litter survival. These differences were the result of differential survival among the litter groups during a three

month period in the fall (September-November). Predation was the primary proximate cause of death for weaned juvenile hares, accounting for 86% (37/43) of deaths. Although the dominant predators of juvenile snowshoe hares were annual residents, avian predation was low after November while mammalian predation was constant from mid-August through April. No collared weaned juveniles died before mid-August.

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GENERAL INTRODUCTION

Snowshoe hares (*Lepus americanus*) are found throughout the boreal forests of North America (Banfield 1974). Through most of their distributional range, hare populations are cyclic. Peak densities occur every 8-11 years, and peaks are synchronous across the continent (Keith 1963, 1990). Although Hudson Bay Company fur return records dating back two centuries give indirect evidence of population cycles (Keith 1963), it is only within the last century that researchers have begun studying the demographic changes associated with hare cycles. The amplitudes of cycles studied to date differ, ranging from a ten fold change in density from low to peak years in Lake Alexander, Minnesota (Green & Evans 1940) to a one hundred fold increase in Rochester, Alberta (Cary & Keith 1979). In all studies, changes in hare survival and reproduction were associated with the changing densities (Keith 1990).

Cyclic fluctuations in the numbers of animals are of interest to ecologists for a variety of reasons. One is the effect such fluctuations have on the community in which cyclic populations live. Since snowshoe hares may account for up to 50% of the herbivore biomass present in boreal forests (Boutin *et al.* 1995), they play an important role in the forest ecology. The classical predator-prey relationship between lynx and hares has been written about for many years (Elton & Nicholson 1942, Ward and Krebs 1985, Breitenmoser *et al.* 1993). However, changes in hare densities affect not only predators. Boutin *et al.* (1995) looked at population levels of 22 species of predators and herbivores through one hare cycle and discovered a correlation between the cyclic hare densities and cyclic population densities in 9 of the other 21 species. Hares may compete with other herbivores directly for food when hare densities are high, and indirectly affect their populations as predators switch to alternate prey when hare numbers are declining (Bergerud 1983). In addition to affecting animals, increases in hare densities can affect the plant population (Keith *et al.* 1984, Smith *et al.* 1988).

A second question ecologists have attempted to answer regarding cyclic populations of mammals is what underlying factors cause the populations to fluctuate in such a predictable

manner. Several hypotheses have been proposed to explain the hare cycle, with the Keith hypothesis and the predation hypothesis receiving the most attention. The Keith hypothesis proposes sequential events that regulate the population. Lack of food during the hare peak causes the initial decline followed by population regulation by predators once food is no longer limiting (Keith & Windberg 1978). Experimental manipulations have tested this theory by adding food to hare populations. Although these studies have resulted in increased hare densities and have delayed the decline, no manipulations have prevented the decline (Krebs *et al.* 1986a, 1986b, 1992).

The predation hypothesis proposes that predators alone regulate the cycle. As hare densities increase, predators respond functionally and numerically and cause the prey populations to decline (Korpimäki & Krebs 1996). As hare numbers decline, predators are forced to migrate, starve, or switch to alternate prey, and thus predation pressure on hares declines. Trostel *et al.* (1987) developed a mathematical model in which predation was sufficient to generate population cycles, yet experimental manipulations (mammalian predator exclosures) have failed to prevent the cyclic decline (Krebs *et al.* 1995).

McNamara & Houston (1987) have demonstrated, using simulation models, the strong interaction between food and predation and conclude that neither food nor predation in isolation regulates populations. Instead, they suggest an interaction between food and predation limits the size of animal populations. Possibly this interaction is in the form of risk sensitive foraging by hares (Hik 1995, Krebs *et al.* 1995). The risk sensitive foraging hypothesis suggests that the factors of food and predators are integrated through the behaviour of the hare to cause the cycle (Hik 1995). Individual hares modify their foraging behaviour in response to changes predation risk. In turn, these foraging decisions can influence body condition, reproduction, and survival.

Other hypotheses to explain hare cycles have received varying degrees of support. Bryant (1981) has shown that after severe browsing by hares at peak population densities, some plant species can produce antifeedants which make the new growth unpalatable. He

suggests that by making this vegetation unpalatable, food shortage occurs despite apparently high food availability. Other factors proposed are infectious diseases, weather (Keith 1990), and tick infestations (Cox 1936). Although there is little evidence that these factors can regulate the hare cycle in isolation, it should be noted that they may contribute to compensatory mortality (Murray *et al.* 1997).

Although the underlying cause of numerical changes in the population are debatable, numerical changes in a population is governed by changes in birth, death, immigration, and emigration rates. Before an accurate model, either conceptual or mathematical, can be developed for snowshoe hare population dynamics, it is necessary to know how each of these four components affects different sectors of the population at various stages of the cycle.

Many factors may affect whether or not an individual disperses away from its natal site or remains to mature and breed there (Stenseth & Lidicker 1992). Gaines & McClenaghan (1980) divide the hypotheses used to explain the proximate causes of dispersal into four categories. The social subordination hypothesis (Christian 1970) suggests that increased social interaction as population density increases will create a situation where dominant individuals will force subordinates to disperse. The genetic-behavioral polymorphism hypothesis is similar to the social subordination hypothesis but includes a genetic component (Chitty 1967, Krebs 1978). The presaturation-saturation hypothesis proposes that under different population densities, different individuals will disperse (Lidicker 1975). At or near carrying capacity, individuals that are "doomed" to die because of limiting factors and social rank will disperse, while below carrying capacity those individuals most sensitive to changes in density will disperse. The final proximate cause of dispersal category is the social cohesion hypothesis, which predicts social interactions prior to emigration, such as interactions with siblings, determine whether or not an individual disperses (Bekoff 1977). Although these theories have been placed into different categories, they are not mutually exclusive (Dobson & Jones 1985).

Juvenile snowshoe hares provide opportunity to determine how date of birth and age may affect both natal dispersal decisions and survival. Adult female hares produce multiple litters in distinct litter groups. The number of litters produced in a summer by each individual varies from two to four and is dependent on the phase of the cycle and date of first litter conception (Severaid 1945, Cary & Keith 1979, Keith 1990). Timing of first litter conception is controlled by both photoperiod and the onset of spring weather conditions and is synchronous within an area (Cary & Keith 1979, Kuvlesky & Keith 1983, Keith 1990, O'Donoghue & Krebs 1992). Leverets (young hares) are born following a gestation period of approximately 37 days, and adult females breed for subsequent litters immediately postpartum (Severaid 1945, Keith 1990).

Leverets leave their natal nest and hide apart from other siblings 1-4 days after being born (Rogstad & Tester 1971, O'Donoghue & Bergman 1992), but stay within 75m of the nest for about 35 days (Rogstad & Tester 1971). They are weaned at the age of 25-28 days, although the last litter of the summer may be nursed longer (O'Donoghue & Bergman 1992), and juveniles disperse any time after weaning (Graf & Sinclair 1987, O'Donoghue & Bergman 1992). In the wild, juvenile hares grow at a fast rate (O'Donoghue & Krebs 1992) and reach adult weight by the age of 6 or 7 months (Dodds 1987).

Since litter groups are spaced five weeks apart, individuals from the different litter groups will face different environmental conditions and experience different levels of juvenile hare densities. In this study, my main objective was to determine if there were differences in the dispersal patterns or survival among the different litter groups born in the summer during the increase phase of the hare cycle.

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CHAPTER 1. JUVENILE HARE DISPERSAL

Introduction

Dispersal can affect population dynamics by influencing genetic structure and establishing new populations (Gaines & McClenaghan 1980, Stenseth and Lidicker 1992a). Dispersal may also be a necessary component in the regulation of some small mammal populations that cycle (Krebs *et al.* 1973, Gaines *et al.* 1979) and prevent some populations of cyclic species from cycling in some locations (Dolbeer & Clark 1975, Buehler & Keith 1982). In order for dispersal to affect population density at a large scale, dispersers and non-dispersers must survive differently. In the literature, it is commonly assumed that dispersers suffer higher mortality than non-dispersers (Christian 1970, Lidicker 1975), but this assumption has rarely been empirically tested (Johnson & Gaines 1990, Van Vuren & Armitage 1994).

For snowshoe hares (*Lepus americanus*), which undergo a 9-11 year population cycle throughout much of their distributional range, dispersal is not necessary for the population to decline (Boutin *et al.* 1985), although dispersal rates may vary during the population cycle. Dispersal appears to be highest during the winters of peak and early decline of populations (Windberg & Keith 1976, Boutin *et al.* 1985). Keith & Windberg (1978), in contrast, found net ingress and egress rates to be highest during the increase phase of the cycle. Part of the discrepancy between these studies may be the result of using indirect methods, such as removal grids and the ratio of immigrants to residents on trapping grids, to quantify hare dispersal. The dispersal rates obtained by these methods may not reflect the true dispersal situation (Dobson 1981, Boutin *et al.* 1985, Koenig *et al.* 1996). This has been shown for hares where, in the same study, results depended on the method used. Boutin *et al.* (1985) found dispersal, measured as the number of immigrants to a removal grid per resident hare on a control grid, was negatively correlated with the rate of population increase, while radio tracking of hares revealed no variation in dispersal through the same time period. The general

aim of this study was radio track individual juvenile snowshoe hares in order to quantify the proportion that emigrate and to determine which factors may influence dispersal.

For animal populations, usually one category of individuals is associated with dispersal. For mammals, juvenile males tend to disperse (Greenwood 1980). Several theories have been proposed to explain why sex-biased dispersal occurs and these focus on competition for mates or resources and inbreeding avoidance (Greenwood 1980, Moore & Ali 1984, Pusey 1987, Johnson & Gaines 1990). Studies of snowshoe hares have been partially consistent with the dispersal trends seen in other mammals. Juveniles are the predominant dispersing group in the species (Windberg & Keith 1976, Keith *et al.* 1984, Boutin *et al.* 1985, Keith 1990), yet only one study, conducted at the peak of the snowshoe hare cycle, has indicated male-biased dispersal may occur within the juvenile cohort (O'Donoghue & Bergman 1992).

Because juveniles are the predominant dispersers, many researchers have stressed the importance of studying natal dispersal at all stages of the hare cycle (Keith 1981, 1990, O'Donoghue & Bergman 1992). For juvenile snowshoe hares dispersal distances may be large (20 km reported by O'Farrell 1965), and movements of 700 m in one night have been recorded (O'Donoghue & Bergman 1992). Juveniles can disperse shortly after weaning (24-28 days old) (Boutin 1984a, O'Donoghue & Bergman 1992) or at any time of the year (Boutin 1979, Keith *et al.* 1984, 1993), but it is unknown how variable these periods of dispersal are and what factors may affect the age at which hares disperse.

Several factors may affect dispersal strategies of individuals, including age and food availability (Stenseth & Lidicker 1992b), but it is unknown if either of these factors affect juvenile hare dispersal. Dispersal behaviour may also vary among litter groups since up to four distinct litters of juvenile hares, spaced approximately five weeks apart, can be produced in a summer (Keith 1990). Each litter group will face different environmental conditions and different densities of conspecifics at the same stage in their life.

Definitions

Various terms have been used by different authors in the dispersal literature. The definitions I have used are as follows:

natal dispersal: “the movement the animal makes from its (birthplace) to the place where it reproduces or would have reproduced if it had survived and found a mate” (Howard 1960)

natal dispersal distance/dispersal distance: the linear distance from an individual's nest site to its breeding location

emigrant: a hare which moves further than 2 adult home range diameters. This distance was used to distinguish home ranges which potentially overlapped with the natal home range from those which did not.

emigration distance: distance moved by hares classified as emigrants. Emigration distances are a subset of dispersal distances

philopatric: a hare which is not classified as an emigrant (i.e. dispersed less than 2 adult home range diameters)

sex-biased dispersal: differences in dispersal distance, proportion of emigrants, or timing of emigration between the sexes

The general aim of this study, which was conducted during the increase phase of a hare cycle, was to obtain baseline information on natal dispersal of individual snowshoe hares using radio telemetry. In an attempt to determine which of the many possible factors may influence dispersal in juvenile hares, I studied males and females from three litter groups on food addition and control areas from the age of five weeks until their first breeding season. Food addition treatments were areas in which commercial rabbit chow had been provided *ad lib.* since 1986. Specifically, my objectives were to quantify 1) the probability that a juvenile would emigrate, 2) natal dispersal distance, and 3) age at emigration, and to determine how these measures differed among litters and for males and females in areas with supplemental

food compared to control areas. Additionally, I wanted to test the assumption that emigration is associated with a high survival cost in juvenile snowshoe hares. Table 1.1 summarizes the factors I studied and predictions of how each would influence natal dispersal.

Methods

General Methods

This study was carried out from June 1995 to April, 1996 in conjunction with the Kluane Boreal Forest Ecosystem Project near Kluane Lake, Yukon Territory (60°57' N, 138° 12' W) . The vegetation in the study area is predominantly white spruce (*Picea glauca*) forest, with an understory of willow (*Salix* spp.), bog birch (*Betula glandulosa*), and soapberry (*Sherphardia canadensis*) (Douglas 1974, Boutin *et al.* 1995).

I studied hares on five areas, two 36-ha control grids (Sulphur-Control 1 and Chitty-Control 2), one off-grid control area (Control 3), and two 36-ha food addition grids (Gravel Pit-Food 1 and Agnes-Food 2, Figure 1.1). On food addition grids, commercial rabbit chow (min. 16% crude protein) was spread *ad lib* every 5-10 days along four equally spaced cut lines running the length of the grids. This treatment began in 1986 and continued year round until April 1996.

Hare trapping

Trapping for juvenile hares began on all study sites in June 1995, when the first litter juveniles were approximately 4-5 weeks old. Each grid contained 400 stations in a 20 X 20 grid system with 30 m between stations and a total of 86 Tomahawk traps (Tomahawk Live Trap Company, Tomahawk, Wisconsin) divided among eight rows (Kluane Project 1995). Traps were baited with alfalfa cubes and apple with the addition of rabbit chow as extra bait on food grids. Traps were set in the evening and checked the following morning. Periodic trapping continued throughout the summer and early fall to capture second, third, and fourth

Table 1.1 Factors studied and predictions for how each may affect juvenile hare dispersal and how emigration may affect survival. Dispersal refers to both dispersal distance and the proportion of individuals emigrating.

Factor	Effect on	Prediction	Reasoning	Source
Sex	Dispersal	male-biased	male-biased dispersal often occurs in small mammals	Greenwood 1980, Dobson 1982, Wolff 1994
Food addition	Dispersal	food < control	increased hare dispersal in peak of cycle, possibly due to food shortage	Windberg & Keith 1976, Boutin <i>et al.</i> 1985
Litter group	Dispersal	later litters may emigrate at an older age or less frequently	later litters may be nursed longer, delaying or reducing emigration	O'Donoghue & Bergman 1992
Age of emigration	Emigration distance	positive correlation between age and emigration distance	hares emigrating at a younger age will face less intraspecific competition and be able to establish closer to the nest site	Boutin 1984b
Emigration date	Emigration distance	positive correlation between emigration distance and date	emigrants will occupy the first suitable vacant habitat they find, therefore those that emigrate earlier have more vacant habitat available to them and will be able to establish in areas closer to their nest site	Waser 1985
Emigration	Survival	emigrants survive less well	high mortality of dispersers relative to non-dispersers in other small mammals	Steen 1994, Byrom 1997

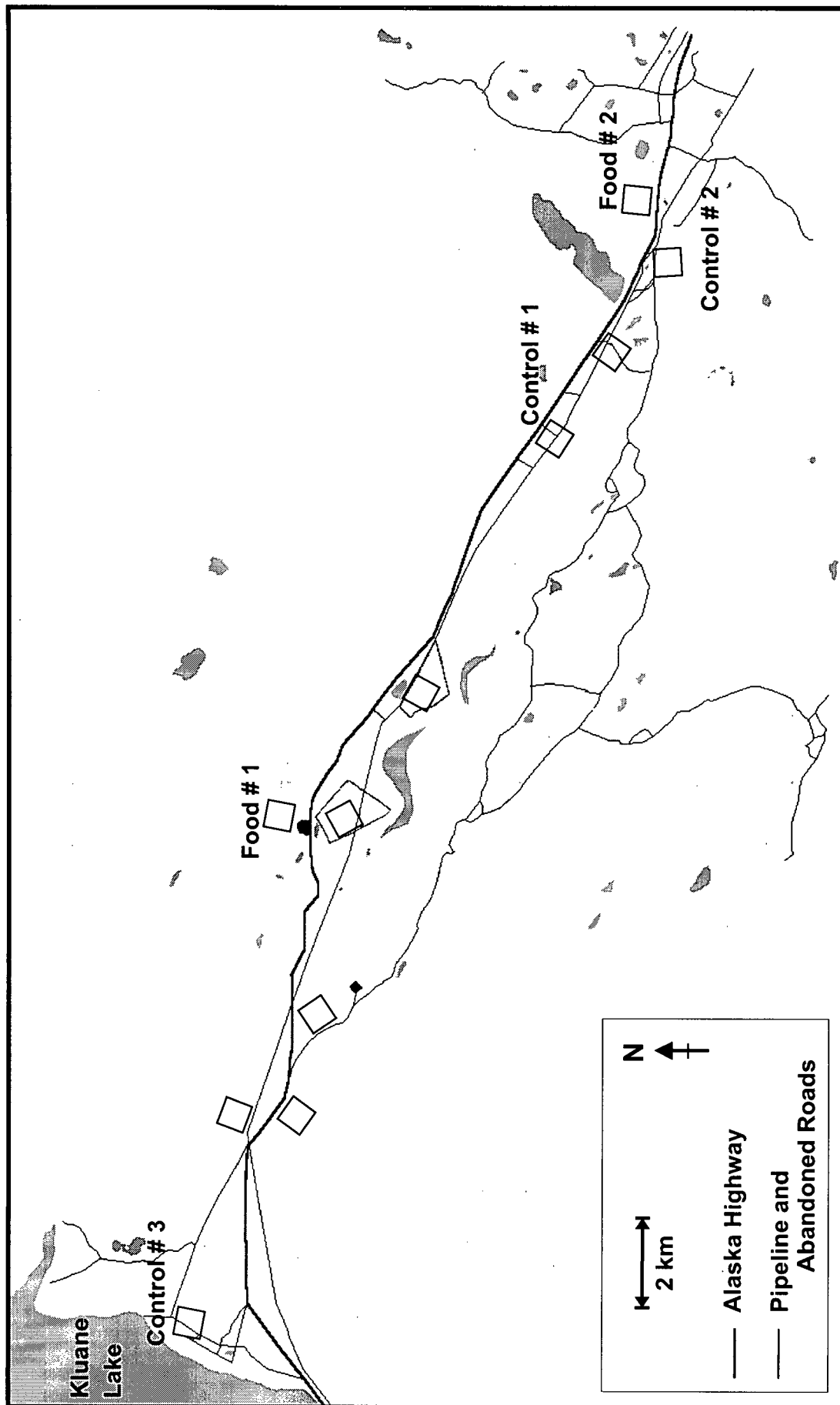


Figure 1.1 Map of study area and study sites. Control # 3 is an offgrid site. Grids not labeled are used by the Kluane Boreal Forest Ecosystem Project but were not used in this study. Map courtesy of A. Kenney.

litter juveniles. From July until October 1995, trapping was suspended on Food 1 due to the persistent presence of a grizzly bear.

The first time hares were trapped, they were eartagged with individually numbered No. 3 Monel tags (National Band and Tag Co., Newport, Kentucky). At every capture, the hare's tag, trap location, weight, length of right hind foot, sex, reproductive condition (female: lactating or not lactating, male: abdominal or scrotal testes), and age (adult or juvenile) were recorded (Kluane Project 1995). Hares were identified as juveniles based on weight, right hind foot length, and male penis shape (Keith *et al.* 1968). I assigned litter group (1-4) to juveniles based on weight and right hind foot length, using measurements of juveniles from known litter groups (tagged at birth by C. Stefan as part of a concurrent study) as a guide.

Collaring procedure

I radio-collared juvenile hares weighing >500g with 25g radio-collars (TW-3 transmitters with 1/2 AA batteries and whip antenna, Biotrack Ltd., Dorset, U.K.) which I had padded with 1.5 cm of foam to allow for hare growth (Byrom and O'Donoghue, manuscript in preparation). Occasionally, smaller hares were collared with lighter collars, but the collar weight never exceeded 5% of body weight. I also collared 5 juvenile hares weighing over 1000g with 40g hare collars (Lotek, Newmarket, Ontario). All collars were equipped with a mortality switch which caused the pulse rate to double if the collar did not move for 3-4 hours. A minimum of 8 hares/litter/treatment (total of 84 individuals) were collared with the exception of fourth litter controls where I collared only 4 hares due to a shortage of radio-collars.

Statistical Analyses

Before analyzing data using parametric tests, I checked data for normality and homogeneity of variances and transformations were done where necessary. I performed logistic regressions on JMP (SAS Institute Inc., Cary, North Carolina) and all other statistical analyses on SYSTAT (Systat Inc., Evanston, Illinois) using $\alpha = 0.10$. Power analysis was

performed on non-significant results using the program nQuery Advisor.

All 28-day survival estimates were calculated using POLLOCK (Krebs unpublished), a program which performs a Kaplan-Meier survival estimate and allows for staggered entry of individuals into the study (Pollock *et. al* 1989). I considered groups to be significantly different if their 90% confidence limits (as calculated by Greenwood's standard error) did not overlap.

Dispersal Methods

Location data

Dispersal distances for all analyses were calculated as the linear distance from the hare's nest site. Hare locations were gathered from three sources: telemetry, mortality, and trapping. All locations were converted to Universal Transverse Mercator (UTM) co-ordinates in order to calculate linear distances.

Nest site locations

I determined a juvenile hare's nest site location in one of two ways. Some of the hares used in my study had been tagged at birth, and for these hares an exact nest site location was known (C. Stefan, unpublished data). For other hares first trapped under the age of 35 days, I used first trap site as the nest site. Previous studies have shown that leverets remain within 75 m of the nest while < 35 days old (O'Donoghue & Bergman 1992), so for hares under this age, I assumed dispersal had not yet occurred. I determined the hare's age at first capture using the mean date of birth for each grid (C. Stefan, unpublished data, Appendix 1). I assumed this method to be reliable as parturition dates are synchronous for females within an area (Keith 1990). Animals which had not been tagged at birth and were first captured older than 35 days were not used in any dispersal analysis. Additionally, as the parturition date for fourth litter was not accurately known, I did not use fourth litter juveniles in the dispersal analysis.

Telemetry locations

I radio tracked juvenile hares and located them visually throughout the summer and fall of 1995 and again during February and March, 1996. I recorded hare location relative to permanent grid stakes for animals on grids, which was accurate to within approximately 5m. For off-grid animals, I recorded the location using a global positioning system (GPS, Trimble Navigation). When corrected for satellite variation, this method was accurate to within 10-30 m, while uncorrected locations were accurate to within 100m. Due to equipment problems, I occasionally determined locations using 1:50 000 topographical maps. The accuracy of this method was similar to that of uncorrected GPS locations.

Mortality locations

Mortality locations were recorded the same as telemetry locations. I did not use mortality locations for collars which had been scavenged by animals other than red squirrels as I could not be certain how close the kill site was to the collar location. Red squirrels have small territories (<0.5 ha) which they defend (Price *et al.*, 1986), so collars scavenged by red squirrels are most likely to have come from nearby. Additionally, if I was uncertain that the hare remains were near the kill site, I eliminated the mortality location from the analysis.

Trapping location

For hares trapped on grids, the trapping location was recorded by its grid stake location. For off-grid traps, trap position was recorded using GPS.

Determination of natal dispersal distances and emigration frequency

Natal dispersal was calculated as the linear distance from the nest site to the animal's spring location. For each hare, I averaged all telemetry, trapping, and mortality locations obtained during February and March to obtain one spring location. Animals that did not survive until February 1996 (one month prior to the breeding season) were eliminated from the analysis.

Statistical analyses

Dispersal distances were compared between treatments, sexes, and among litters using nonparametric analysis (Kruskal-Wallis test). Dispersal distances between sex and treatments were also compared using logistic regression (Trexler & Travis 1993). To determine if the proportion of individuals emigrating varied among sex, treatment, and litter, I performed a log linear analysis.

Determination of emigration age and date

Every time a collared juvenile was located, either by telemetry, trapping, or mortality, I calculated the linear distance of the hare's location to its nest site. The number of locations per animal ranged from 2 to 34 (mean of 12). In this way, I was able to determine the date at which an individual hare first moved further than two home range diameters from its nest site. I converted date to age by subtracting the mean date of birth for each litter on each grid (C. Stefan unpublished data, Appendix 1) from the movement date. Individuals were not located on a daily basis, so I calculated minimum and maximum age and date of dispersal and used the median value in the analysis. If the difference between minimum and maximum age of dispersal was greater than one week, I eliminated the hare from the analysis as the true date of dispersal was too uncertain.

I classified movements of greater than two home range diameters from the natal nest as one of two types: forays or emigration. A hare which made a foray moved further than two home range diameters from the nest site, but returned to within two home range diameters of the nest site within one week. Emigration occurred if the hare remained further than two home range diameters from the natal nest for a minimum of four weeks. No hares moved greater than two home range diameters and returned to the nest site location between two to four weeks later. All animals that exhibited a emigration movement were included in this analysis, even if they did not survive until spring.

Statistical analyses

I performed an ANOVA on log transformed data, using log (age of emigration) as the dependent variable. Due to small sample sizes, only main effects (litter, sex, treatment) were examined. Correlation analysis was performed on the relationships between age and date of emigration with emigration distance (either natal dispersal distance or distance from nest site to mortality site).

Determination of the survival cost of emigration

All juvenile hares for whom a nest site was determined and which were not censored (collars removed or signal lost) before the end of the study were used in this analysis. For hares which survived until the end of the study, dispersal distance was natal dispersal distance. For hares which died before the end of the study, dispersal distance was calculated as the linear distance between nest site location and mortality location.

Statistical analyses

To determine if a correlation existed between distance from nest site and fate (dead or alive) logistic regression was performed (Trexler & Travis 1993). Twenty-eight day survival and 90% confidence limits of emigrants and philopatric individuals were estimated using POLLOCK (Krebs unpublished). The proportions of emigrants and philopatric individuals dying and surviving for each sex, litter, and treatment were compared using log linear analysis.

Sample Sizes

A breakdown of the sample sizes for each of the analyses is provided in Figure 1.2. Of the 84 juvenile hares collared, I was able to establish nest site locations for 35 (cost of emigration analysis). Of these 35, 18 survived until February, 1996 and were used to analyze natal dispersal distance. Eighteen of the 35 hares were classified as emigrants and could be used to analyze the age of emigration. One of these individuals returned to his natal site after

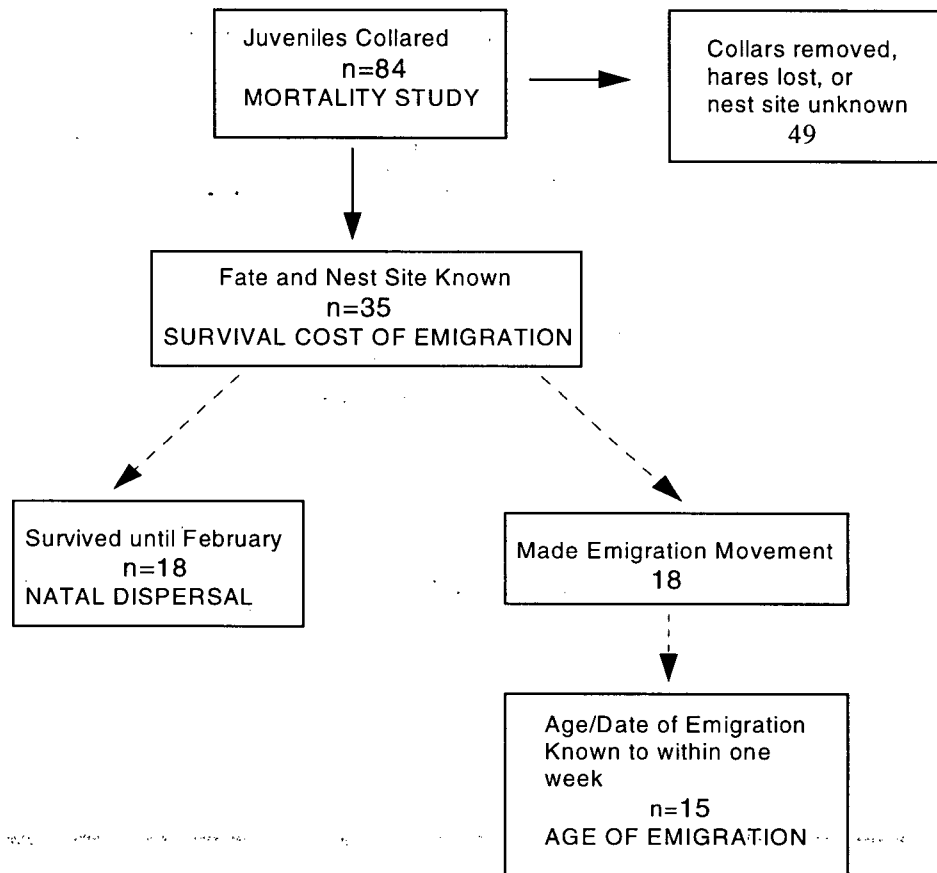


Figure 1.2 Flow chart showing sample sizes used in each analysis. Solid lines represent a breakdown of samples while broken lines represent a sub-set of hares.

several months and was therefore included in the age of emigration analysis but classified as a philopatric individual in the natal dispersal analysis.

Results

Hare Densities

Hare population densities on both food and control treatments changed in a cyclic manner with a population increase, peak, and decline from 1987-1993 (Figure 1.3). My study took place during the early increase phase of the hare cycle (1995-1996). Hare densities on the food grids were approximately twice that of the control grids during the course of my study.

Natal Dispersal

Natal dispersal distances varied greatly among individuals and ranged from 23 m to over 16 km (Figure 1.4). Fifty percent of juvenile hares emigrated (minimum distance to be classified as an emigrant: males > 812 m, females > 554 m (Appendix 2)). Table 1.2 provides a more detailed breakdown of the proportion of emigrants based on litter, treatment, and sex.

Control populations showed no evidence of sex-biased dispersal, but male-biased dispersal occurred on the food treatment areas (Figure 1.4). Natal dispersal distances did not vary among the litter groups (K-W test statistic = 0.46, $p=0.80$ with 2 df) so litter groups were combined for analysis. Within the control group, there was no statistically significant difference between the distance dispersed by males and females (Figure 1.4) or the proportion of males and females emigrating (Table 1.2), and no relationship was found between sex and dispersal distance (logistic regression: $r^2=0.07$, $\chi^2=1.09$; $p=0.30$ with 1 df). On food addition areas, males dispersed significantly farther than females (Figure 1.4) and emigrated in

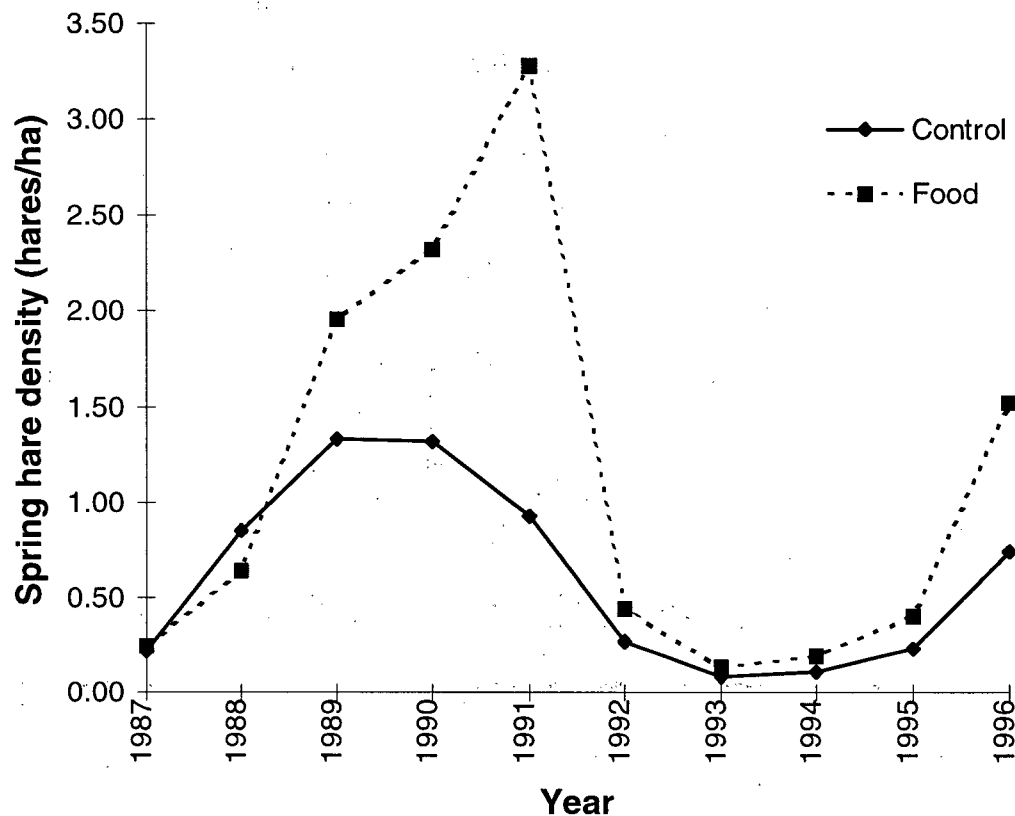


Figure 1.3 Spring hare densities on control and food addition grids (Krebs *et al.* 1995, Krebs unpublished data). Hare densities were calculated using CAPTURE (White *et al.* 1982) and an effective trapping grid area of 60 ha. Control represents average density on Controls 1 and 2 and food is an average of densities on Foods 1 and 2. Spring hare densities on food grids were 1.7 times higher than controls in 1995 and 2.1 times controls in 1996. This study was conducted during the early increase of the hare cycle (June 1995-April 1996).

Figure 1.4 Natal dispersal distances for juvenile hares that survived until spring (n=18). Note scale change after x-axis break. On the food treatment, males dispersed significantly further than females (Mann Whitney U=0.0; $\chi^2=3.43$; p=0.07 with 1 df) but not on controls (Mann Whitney U=16; $\chi^2=0.00$; p=1.00 with 1 df). Neither male nor female natal dispersal distance differed between treatments (males: Mann Whitney U=12.0; $\chi^2=0.46$; p=0.50 with 1 df, females: Mann Whitney U=6.0; $\chi^2=0.86$; p=0.36 with 1 df). Although median dispersal value for females was lower on food addition areas than controls and male median dispersal distance was larger on control than food addition areas, the difference was not significant in either case (females: $\chi^2=2.50$, p=0.11 with 1 df; males: $\chi^2=1.79$, p=0.18 with 1 df).

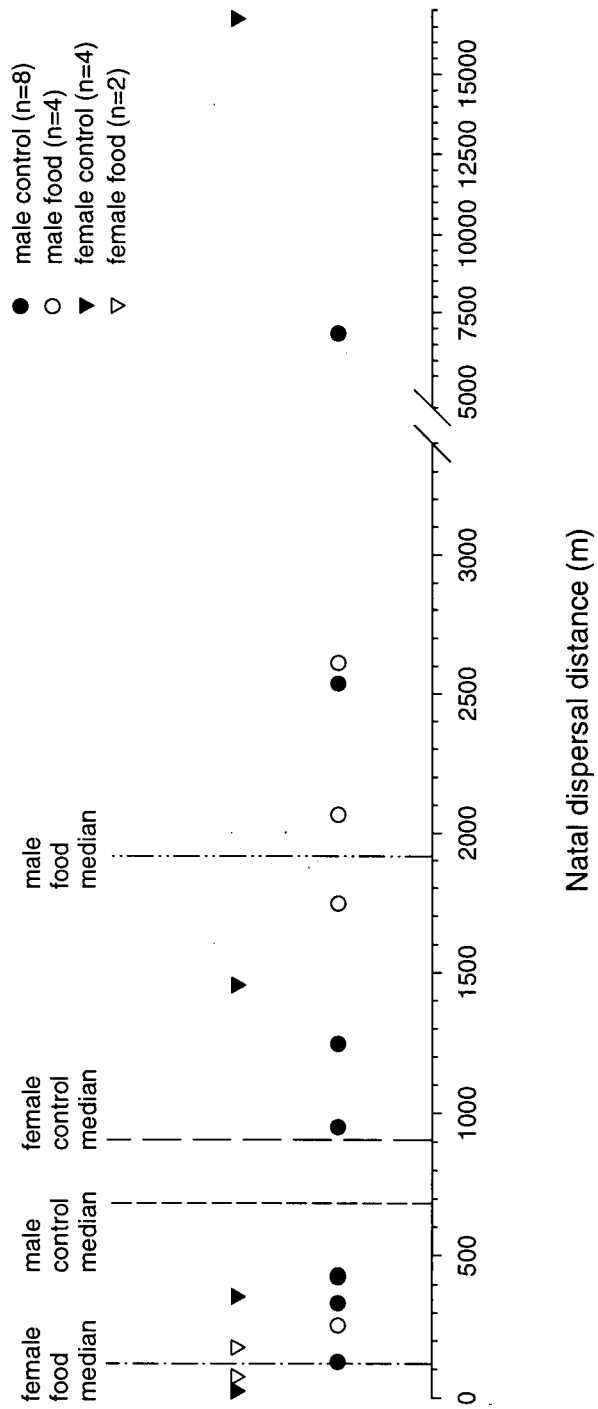


Table 1.2 Proportion of juvenile hares that emigrated from their natal home range before their first breeding season. Males had to disperse 817 m from their nest site to be classified as an emigrant, while females had to disperse 554 m (Appendix 2). Significantly more males than females emigrated on the food treatment (Pearson $\chi^2=3.00$; $p=0.08$ with 1 df) but not on controls (Pearson $\chi^2=0.00$; $p=1.00$ with 1 df). There was no difference in the proportion of each sex emigrating between the two treatments (males: Pearson $\chi^2=0.69$; $p=0.41$ with 1 df, females: Pearson $\chi^2=1.50$; $p=0.22$ with 1 df).

Treatment/Litter	n	Number of Emigrants	Proportion of Individuals Which Emigrated
All Juveniles	18	9	0.50
Control			
male	8	4	0.50
female	4	2	0.50
Food			
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

greater proportion than females (Table 1.2), and a significant relationship existed between sex and dispersal distance (logistic regression: $r^2 = 1.00$, $\chi^2 = 7.64$; $p = 0.006$ with 1 df).

Although males dispersed farther than females on food treatments but not controls, no difference in dispersal distances or proportion of emigrants was detected between food addition and control areas within a sex (Figure 1.4, Table 1.2). The range of dispersal distances was less for both males and females on food addition areas than on control areas.

Timing of Emigration and Foray Activity

Litter 3 juveniles emigrated at an older age than juveniles from litters 1 and 2, but neither treatment nor sex significantly affected age of emigration (Figure 1.5). Although a significant positive correlation existed between emigration distance and age of emigration, the same relationship was not seen between emigration distance and date of emigration unless the outlier was removed from the analysis (Figure 1.6). Therefore, the relationship between emigration date and distance is reliant upon the presence of an atypically large dispersal distance. Over the majority of dispersal dates and distances, no relationship was detected.

Some hares exhibited exploratory movements before dispersing. Forays were observed in three hares, two of which emigrated two and ten days after the foray had been made, while the third survived until the end of the study but did not emigrate. One individual dispersed approximately 900 m from its nest site at 62 days of age and later returned (between 127 and 265 days of age) to his natal area.

Survival of Emigrants

Although survival of emigrants tended to be lower than for philopatric individuals, the difference was not significant. There was no significant difference between treatments, sexes, or among litters in the proportion of emigrants or philopatric individuals dying (Table 1.3, more detailed breakdown provided in Appendix 3) or 28-day survival (Table 1.4) so litters, sexes, and treatments were combined for the rest of the analyses. There was no significant difference in the proportion of emigrants and philopatric individuals dying (Table 1.3), but I

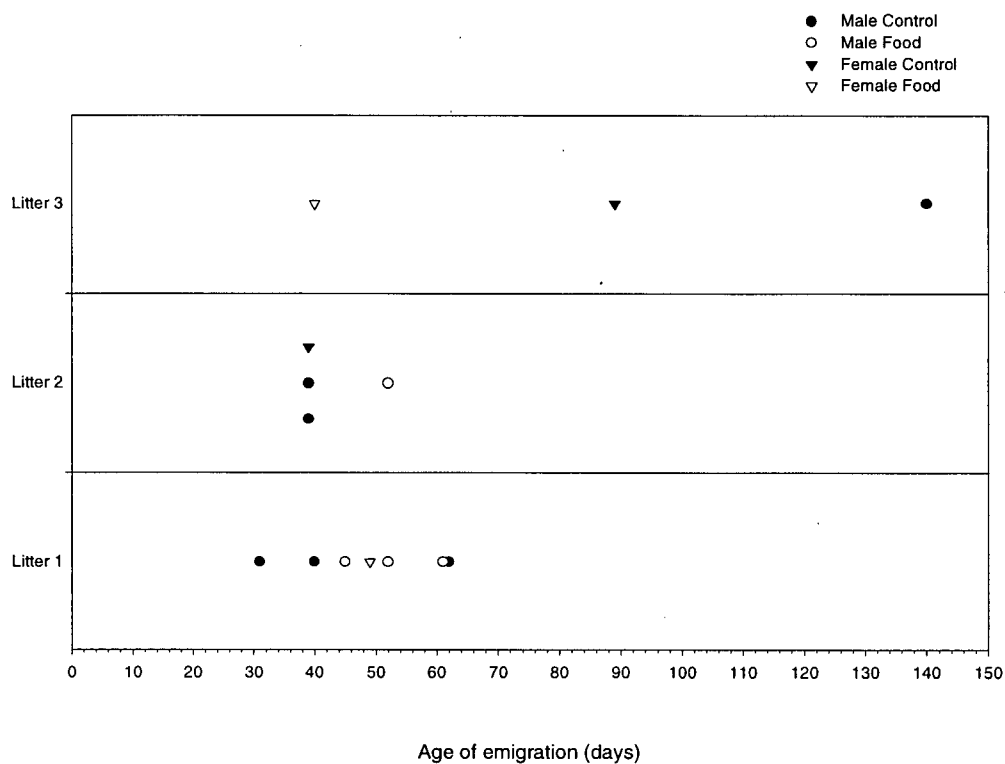


Figure 1.5 Age at which juveniles emigrated. Litter 3 juveniles emigrated at a significantly older age (mean 84 days; 90% C.L. 53-130 days) than first and second litter juveniles (mean 48 (41-55) and 42 (37-47) days). No difference in age of emigration was evident between food and control treatment, or between males and females (treatment: f-ratio = 0.001, $p=0.97$ with 1 df, sex: f-ratio = 2.17, $p=0.17$ with 1 df, litter: f-ratio = 6.24, $p=0.02$ with 2 df).

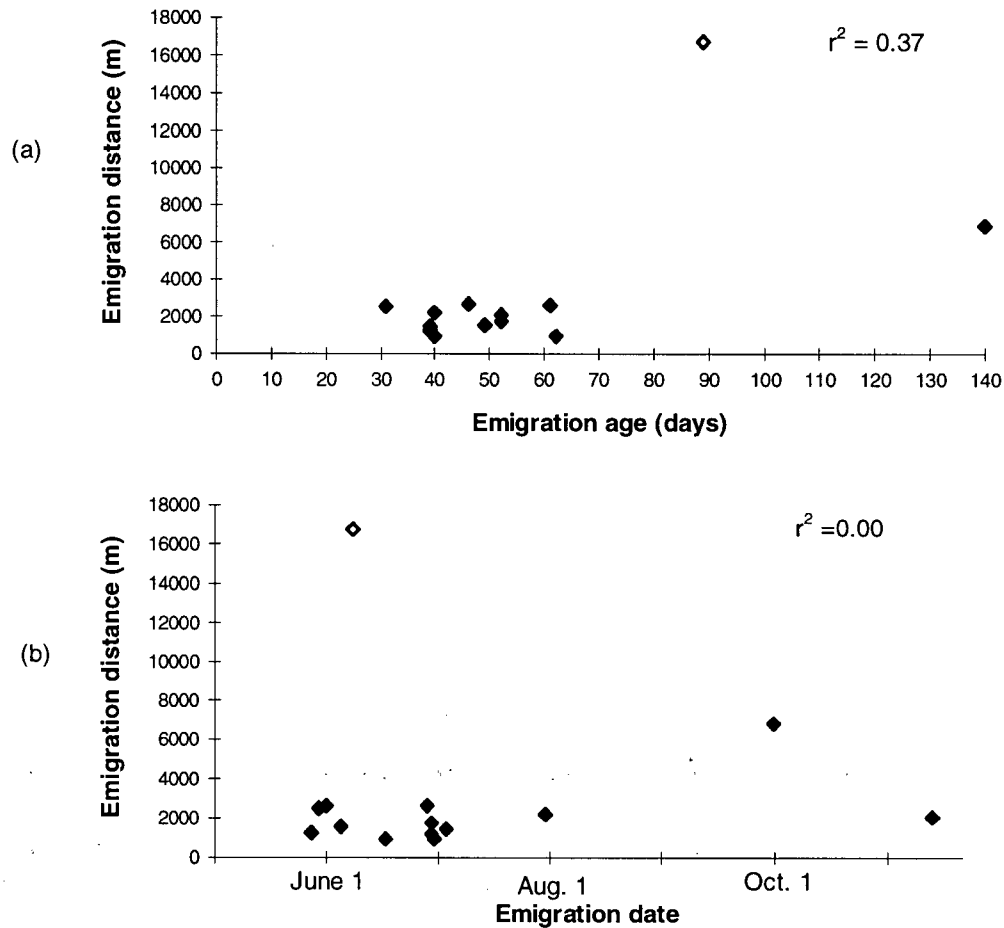


Figure 1.6 Relationship between emigration distance and (a) age of emigration and (b) date of emigration. Pearson correlation coefficients are given and the outlier is indicated by the open symbol. Emigration distance is significantly correlated with age at dispersal (with outlier: Pearson's $r^2 = 0.37$ $p = 0.02$, without outlier: Pearson's $r^2 = 0.75$ $p < 0.001$) but not date of dispersal (Pearson's $r^2 = 0.00$ $p = 0.97$) unless the outlier is removed (Pearson's $r^2 = 0.24$ $p = 0.09$).

Table 1.3 Proportion of emigrants and philopatric individuals that died before the end of the study period. There was no significant difference between treatments, sexes, or among litters in the proportion of emigrants or philopatric individuals dying (log-linear analysis: Pearson $\chi^2 = 12.35$; $p=0.87$ with 19 df), so litter, treatment, and sexes were combined. There was no difference in the proportion of emigrants and philopatric individuals dying (Pearson $\chi^2 = 0.85$; $p=0.36$ with 1 df).

Treatment/Litter	n	Number Dying	Proportion Dead
EMIGRANTS			
Litter 1	7	5	0.714
Control	3	1	0.333
Food	4	4	1.000
Litter 2	4	2	0.500
Control	3	2	0.667
Food	1	0	0.000
Litter 3	6	5	0.833
Control	4	3	0.750
Food	2	1	0.500
Combined	17	12	0.706
PHILOPATRIC INDIVIDUALS			
Litter 1	2	0	0.000
Control	2	0	0.000
Food	0		
Litter 2	6	2	0.333
Control	4	1	0.250
Food	2	1	0.500
Litter 3	10	8	0.800
Control	7	7	1.000
Food	3	1	0.333
Combined	18	10	0.556

Table 1.4 Twenty-eight day survival estimates for emigrating and philopatric juvenile hares as calculated by POLLOCK (C. Krebs unpublished). Survival did not differ between treatments within a litter or among litters for either dispersers or philopatric individuals. Data from all dispersers and all philopatric juveniles were combined and 28-day survival of dispersers did not differ significantly from philopatric individuals.

Treatment/Litter	n	28-day survival estimate	90% Confidence Limits
EMIGRANTS			
Litter 1	7	0.89	0.60-0.95
Control	3	0.96	0.86-1.00
Food	4	0.81	0.00-0.90
Litter 2	4	0.93	0.77-0.99
Control	3	0.89	0.00-0.97
Food	1	1.00	1.00-1.00
Litter 3	6	0.65	0.00-0.78
Control	4	0.71	0.00-0.88
Food	2	0.63	0.00-0.87
Combined ¹	17	0.81	
PHILOPATRIC JUVENILES			
Litter 1	2	1.00	1.00-1.00
Control	2	1.00	1.00-1.00
Food	0		
Litter 2	6	0.94	0.85-1.00
Control	4	0.97	0.90-1.00
Food	2	0.92	0.00-1.00
Litter 3	10	0.62	0.00-0.72
Control	7	0.55	0.00-0.67
Food	3	0.89	0.00-1.00
Combined ¹	18	0.84	

¹ combined survival estimated by equal weighting by litter group:

$$\text{combined} = (\text{litter 1 survival} \times \text{litter 2 survival} \times \text{litter 3 survival})^{1/3}$$

had a power of only 23% to detect a 15% difference. There was also no detectable difference in 28-day survival between emigrants and philopatric individuals (Table 1.4). The apparent discrepancy between the magnitude of the difference in survival between 28-day survival (3%) and the proportion of emigrants which die (15%) arises because hares had to live several months before reaching sexual maturity. Table 1.3 accounts for this time (15 % difference in the proportion dying between weaning and sexual maturity), while Table 1.4 does not (3% difference in survival each month). Logistic regression also showed no significant relationship between dispersal distance and fate (alive or dead) ($r^2=0.01$; $\chi^2=0.52$; $p=0.47$ with 1 df

Discussion

In this study, natal dispersal distance of snowshoe hares was highly variable but emigration was common. Dispersal distance ranged from 23 m to over 16 km, with 50% of juvenile hares emigrating (i.e. dispersing greater than two home range diameters away from their natal nest site). 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 a female was shot 20km (12.5 miles) from her original trap location. A dispersal distance of 33 km for the Arctic hare (*Lepus timidus*) has been documented (Marcström *et al.* 1989). Although such long distance dispersal for hares may be rare, such distances are probably not unique. Past methods which have been used to study animal dispersal, such as trapping grids, tend to underestimate dispersal distances (Koenig *et al.* 1996).

The frequency of emigration in this study is also much higher than that found by other researchers who monitored the dispersal of individual hares. Boutin *et al.* (1985) reported a maximum loss due to dispersal of 28% during the decline phase of the hare cycle and Keith *et al.* (1993) reported only 2.5% (5/194) dispersal in a non-cyclic population. The large difference between my results and those in the literature may be real differences in movement rates between the studies or and artifact of the methods used. Previous studies did not

separate juveniles and adults when calculating dispersal (emigration) frequency. Dispersers are mostly juveniles (Windberg & Keith 1976, Keith *et al.* 1984, Boutin *et al.* 1985, Keith 1990), therefore these earlier estimates probably overestimate adult and underestimate juvenile emigration. Since most hare dispersal studies have not reported the numbers of juveniles which have been radio-collared relative to adults, it is impossible to compare my value of 50% emigration directly to published values. One exception is Boutin's (1979) study, conducted during the increase phase of another hare cycle in the same study area as this study. He reported that 28% of juvenile hares (9 of 32 individuals with radio-collars) dispersed between August 14 and March 31. This estimate included animals which died on grids before their first breeding season, so provides a minimum estimate as it is unknown whether those animals would have dispersed before breeding. The maximum estimate of dispersal, assuming the 12 animals which died on grid would have dispersed before breeding, is 66% (21 of 32).

The only other estimate of natal dispersal frequency was measured as the proportion of recruits to a control area which had not been born in that area (Boutin 1984a). Resident juveniles were identified by the presence of radio-active calcium in their bones. Boutin (1984a) had implanted all females in the area with radio-active calcium prior to parturition which was then passed from mother to offspring. In each of two years during peak hare densities 70% of juveniles trapped in November were classified as immigrants, supporting my results that natal dispersal can be common. This value is higher than my value of 50% emigration, suggesting dispersal rates may be higher during the peak of the hare cycle.

Effects of food, sex, and litter on dispersal

Table 1.5 summarizes the results of this study and compares them to predications of how food, sex, litter, age, and date of emigration may affect natal dispersal in hares.

Table 1.5 Summary of predictions and results regarding snowshoe hare natal dispersal. No effect refers to no statistically detectable effect.

Factor	Effect on	Prediction	Result
Sex	Dispersal	Male-biased	Food : Male-biased Control: No effect
Food addition	Dispersal	Food < control	No effect on dispersal proportion or distance, effect on sex-biased dispersal (male-biased dispersal on food addition)
Litter group	Dispersal	Litters born later in the summer disperse at an older age	Third litter juveniles disperse at a older age than first and second litter juveniles
Age of emigration	Emigration distance	Positive correlation between age and emigration distance	Weak positive correlation between age and dispersal distance
Emigration date	Emigration distance	Positive correlation between emigration date and dispersal distance	No correlation unless outlier is removed
Emigration	Survival	Dispersers survive less well	No effect

Food addition

Contrary to my predictions, I detected no effect of food addition on either dispersal distance or the proportion of juveniles which emigrated. My predictions were based on Boutin *et al.* (1985) and Windberg & Keith (1976) who attributed increased rates of dispersal during peak hare densities to over-winter shortage of food. In their studies, dispersing hares were lighter, smaller, and in poorer condition than non-dispersers. One reason why the food addition treatment may have had no observable effect in this study is that food may not be limiting during the increase phase of the hare cycle. This suggestion is supported by two pieces of evidence. Body condition of adult male hares, based on the relationship of body mass to skeletal size (length of right hind foot), did not differ between food and control grids in the fall of 1995 (Appendix 4). Winter diet quality was measured by fecal fiber as well as nitrogen and fiber intake (based on the quantity and quality of twigs browsed by hares) by K. Hodges (unpublished data). Diet quality on controls was no lower than that on food grids. Previous studies have also indicated that there is ample winter food available during the early increase phase of the hare cycle (Keith 1990). Additionally, it is possible that the lighter weights reported by Boutin *et al.* (1985) and Windberg & Keith (1976) were an artifact of a disproportionately high proportion of juveniles in the dispersing population which would reduce mean weight of dispersers relative to the rest of the population.

Sex-biased dispersal

Male-biased natal dispersal is common for most species of mammals (Greenwood 1980, Dobson 1982), yet in this study dispersal distances, emigration frequencies, and timing of emigration did not differ between males and females on control grids. Proximate causes of sex-biased dispersal include competition for mates, competition for resources, and social interactions (Christian 1970, Gaines & McClenaghan 1980). However, I did not measure any of these factors and therefore in the absence of sex-biased dispersal can only speculate that males and females were not influenced by them differently. The increase phase of the cycle is

characterized by high food availability and moderate hare density (Keith 1990, C.J. Krebs & A.R.E. Sinclair, unpublished data), and as a result resources and mates may have been abundant and interactions with other hares low.

Male-biased dispersal occurs in European rabbits (Kunkele & Von Holst 1996), but in most snowshoe hare studies no sex-biased dispersal has been detected (Windberg & Keith 1976, Boutin 1979, Boutin 1984a). An exception is O'Donoghue & Bergman (1992) who reported that male-biased dispersal (defined by the timing of dispersal and the proportion of each sex which bred on their natal grid the following year) may have occurred during the peak of the hare cycle. A relationship between sex and age of dispersal has also been documented in ground squirrels, in which males disperse earlier and more frequently than females (Downhower & Armitage 1981, Holekamp 1984).

Although male-biased dispersal appears to be the trend for mammals, there are many exceptions. Equal male and female natal dispersal occurs in Arctic hares (*Lepus timidus*- Marcström *et al.* 1989), several species of voles, (*Microtus* spp.- Myers & Krebs 1971, Krebs *et al.* 1976, *Clethrionomys glareolus* - Kozakiewicz 1976) and tree squirrels (*Sciurus carolinensis*- Thompson 1978, *Tamiasciurus hudsonicus*- Larsen 1993 in Larsen and Boutin 1994).

Food addition and sex-biased dispersal

I had no reason to expect that food addition would have any influence on sex-biased dispersal unless food was a proximate cause of sex-biased dispersal and was limiting. However, sex-biased dispersal did occur on the food grids but not the control grids. Since I had small sample sizes for dispersal on food grids (2 females, 4 males), I cannot be certain that my sample was representative of the population, and although I will discuss this result in general terms, it is important to realize it may be a sampling artifact.

Two factors may have been responsible for the differences seen on food and control grids: the addition of food and the increased hare densities associated with food addition. For

reasons previously stated, it is unlikely food was limiting at this phase of the hare cycle. Therefore, it is most likely the differences between the treatments were the result of increased density as opposed to increased food availability. The presence of male-biased dispersal could be the result of social interactions, which may play a role in hare emigration by influencing the ability of individuals to settle into new populations (Boutin 1984a, 1984b, Graf & Sinclair 1987). Additionally, studies of enclosed populations of snowshoe hares show that aggressive hare interactions increase with increased hare density when food is not limiting and that the rate of aggressive interactions may differ between the sexes (Graf 1985, Ferron 1993). It is therefore possible that social interactions caused the sex-biased dispersal seen on the high density food grids. Additional evidence that male-biased dispersal may be related to hare density is that male-biased dispersal has only been seen at the cyclic peak, when hare densities are at their highest (O'Donoghue & Bergman 1992). However, since I did not directly investigate the proximate cause of natal dispersal in this study, the relationship between density and the presence of sex-biased dispersal is correlative, and I cannot be certain that factors other than density did not differ between food and control treatments.

A relationship between density and sex-biased dispersal may also exist in meadow voles (*Microtus pennsylvanicus*), where the percentage of losses from a control grid due to dispersal were similar for males and females except at peak vole densities (Table 6 in Myers & Krebs 1971). Additionally, the proportion of young females which dispersed varied through the cycle, with the highest dispersal rates occurring during the decline, while male rates were constant through the cycle for both *Microtus pennsylvanicus* and *Microtus ochrogaster* (Myers & Krebs 1971). I therefore hypothesize that in cyclic small mammals sex-biased dispersal will be observed only during peak population densities and possibly the decline.

Litter group

Litter group did affect the mean age at which individuals emigrated, with first and second litter individuals emigrating at a younger age than third litter individuals. Females may

nurse their last litter of the season longer and since all females did not produce a fourth litter, some third litter individuals may have been weaned at an older age than first and second litter individuals (O'Donoghue & Bergman 1992). Additionally, growth rates prior to weaning varies significantly among litter groups at peak hare densities (O'Donoghue & Krebs 1992). If weight serves as a cue for dispersal, this differential growth rate may result in the different ages of dispersal. However, given the linkage between age and weight it would be difficult to distinguish which serves as the cue for dispersal.

The differences in the age of emigration between third litter and first and second litters have not been reported elsewhere for hares. However, such differences have been suggested for voles (Beacham 1979). As with the hares in this study, litters born earlier in the year (spring and summer) dispersed at the same age while litters born in the fall either did not disperse or dispersed at an older age. However, in the vole study, juveniles born later in the fall over-wintered in their natal area. Other hare studies have reported first and second litter juvenile hares emigrating throughout the winter (Boutin 1979, Windberg & Keith 1976, Keith *et al.* 1984, Keith *et al.* 1993), but only one of 8 first litter juveniles emigrated in winter in this study, and its age at emigration was not known to within a week. All other juveniles emigrated before November, most between June and August (Appendix 3). In contrast, Boutin (1984a) trapped the largest number of new juvenile immigrants to control areas from September to November during the peak of the hare cycle. This may imply a difference in timing of emigration between the two phases of the cycle, differences in the dispersal rates of different litters during the phases of the cycle, or simply be an artifact of the different methods used in the studies.

Effects of emigration age and date on emigration distance

The presence of a significant positive correlation of emigration age with emigration distance is predicted from the literature, with the explanation that individuals who disperse at a younger age have a better chance of finding and becoming established in vacant territories or

habitats closer to their natal home range (Waser 1985). Although snowshoe hares are not territorial, they do exhibit spacing behaviour (Boutin 1980, 1984a) and emigrating snowshoe hares that arrive later may have more difficulty becoming established as residents (Boutin 1984a, Graf & Sinclair 1987), suggesting that the same correlation may exist. In multi-littered species, this theory would also predict that a positive correlation should exist between date of emigration and emigration distance. I found no such correlation between date of dispersal and dispersal distance unless the outlier is removed (Figure 1.6 (b)). Although I found a significant positive correlation between age and dispersal distance, this was reliant upon either the presence of the outlier (an atypically large dispersal distance) or the inclusion of an animal which dispersed much at a much older age than the others (140 days). In the age range over which most hares dispersed (30 to 60 days), there was no relationship between age and distance of dispersal. I therefore classify this relationship a weak one at best. The weak relationship indicates that emigration distance may be determined by factors other than the location of nearest available habitat, and competition may not be the primary factor in settlement decisions made by snowshoe hares at the increase phase of the hare cycle.

Forays and exploratory behaviour have been documented for species of ground squirrels and red squirrels, and such behaviour may be part of the decision-making process before individuals disperse (ground squirrels, Hackett 1987; red squirrels, Larsen & Boutin 1994, Sun *in review*). The foraging behaviour exhibited by some hares in this study has also been described by Boutin (1984b) and Boutin *et al.* (1985).

Survival of emigrants

Although not statistically different, emigrants appeared to have a lower survival than philopatric individuals. When looking at the proportion surviving until sexual maturity, this difference was 15%. This value is large, but is probably biologically insignificant. The number of emigrants dying was 12 of 17 and the number of philopatric individuals dying was 10 of 18 (Table 1.3). The maximum difference in terms of the number of hares dying is three.

Such a small difference could easily result from natural variation. In other species where a survival difference between dispersers and non-dispersers has been established, the difference in survival is typically greater than 30% (Garrett & Franklin 1988, Steen 1994, Byrom 1997), a difference I had a power of 75% to detect.

Since emigrating hares did not have a higher mortality rate than "stay at homes", the potential for emigration to play a direct role in the regulation of hare numbers at the increase phase of the hare cycle is small. It would appear that at this phase of the cycle, emigration may play more of a role in the expansion of populations, possibly increasing the types of habitat used. If refuges are used by hares during the cyclic low, successful emigration at this phase of the cycle is required for the re-occupation of many of the less optimal habitats (Wolff 1980, 1981).

For hares, there has been no indication of a survival cost to emigration in cyclic populations (Boutin 1984a, Keith *et al.* 1984) and my results are consistent with this conclusion. There is some suggestion that dispersal may be associated with a survival cost in non-cyclic hare populations (Sievert & Keith 1985, Keith *et al.* 1993). In some other species of small mammals, dispersers have suffered higher mortality rates than non-dispersers (ground squirrels, Hackett 1987 and Byrom 1997; prairie dogs, Garrett & Franklin 1988; root voles, Steen 1994) while in other species, they did not (red squirrels, Wauters *et al.* 1994; marmots, Van Vuren & Armitage 1994; kangaroo rats, Jones 1986; common vole, Boyce and Boyce 1988).

Some of the variation between studies may be a result of the time period over which the survival of emigrants is monitored. In some studies, only the period of time that the animal was moving to the new location was considered (e.g. Garret and Franklin 1988) while others consider survival until the age of first reproduction (Boyce & Boyce 1988, Wauters *et al.* 1994) or even longer (Hackett 1987). I calculated survival until the first breeding season, and thereby included any survival benefits, such as increased habitat quality, that may be associated with the new home range. Additionally, these species of small mammals have

different life histories, social structures, and dispersal strategies, all of which may influence risks associated with emigration.

It is important to note that I used only one measure (short term hare survival) in examining the cost of dispersal. Other costs have been documented in ground squirrels. These include reduced reproductive fitness, and non-immediate mortality costs (Hackett 1987, Byrom 1997). Given the high proportion of emigrants in hares during the early increase phase of the cycle, such costs may impact the population, and are therefore worthy of future investigation.

Potential biases in my study

One of the problems associated with dispersal studies is defining who is an emigrant since dispersal distances are continuous. I attempted to avoid this problem by analyzing dispersal distance using logistic regressions (Trexler & Travis 1993), which allowed me to treat dispersal distance as a continuous variable while treating other variables as categories (e.g. emigrants and philopatric individual). The similarity of the results from logistic regression and log linear analysis indicates that my definition of emigrant did not affect the results I obtained.

Several different procedures have been used to define dispersers in other studies (e.g. hares trapped on a removal grid (Boutin *et al.* 1985), hares moving >150m from nest (O'Donoghue & Bergman 1992), hares moving >1.5 km (Keith *et al.* 1993)). In this study, as in Keith *et al.* (1984), a juvenile hare was classified as an emigrant if its natal dispersal distance was greater than two adult home range diameters away from its nest site location, although in this study this distance was 554 m for females, 812 m for males, while two home range diameters in Keith *et al.*'s study was only 400 m for both sexes. This definition ensured that emigrants did not have home ranges which overlapped with their natal home ranges. A more accurate definition of an emigrant is an individual which leaves an established home range to permanently occupy a new non-overlapping home range (Lidicker 1975). Boutin

(1979) used this definition for snowshoe hares. I would have misclassified only two out of ten emigrants in his study (average adult home ranges were calculated from Figures 12 and 13, Boutin 1979) as they had dispersal distances 20m shorter than two home range diameters. In my studies, all hares had natal dispersal distances at least 100 m further or shorter than the distance I had set as the cut-off point. I am therefore confident that I have correctly classified emigrants.

In order to ensure my results were not biased by treating siblings as independent samples (Hilborn 1975, Beacham 1979, Massot *et al.* 1994), I compared variance in log transformed dispersal distance among siblings (6 sibling groups) to the variance among non-related juveniles. In only one case were the variances significantly different. In this case, between sibling variance was higher than non-sibling variance, so I concluded siblings were effectively independent samples.

I defined natal dispersal as the movement of a hare from its nest site location to the place where it would reproduce (as Howard 1960) and defined the place of reproduction as the hare's location in February. Some juveniles may have dispersed immediately after weaning (as young as 24 days old, O'Donoghue & Bergman 1992) or after I obtained their spring location but before breeding, resulting in an erroneous nest site or breeding location. Additionally, it is possible that some juveniles may have bred in their first summer, as scrotal juvenile males were trapped (two first litter juveniles, one second litter juvenile), resulting in their place of first reproduction being their summer location. However, even if it occurred, juvenile reproduction would add little bias to my results since very few juveniles born in 1995 would have reproduced before the 1996 breeding season. Studies in Alberta have found only low rates of juvenile breeding in snowshoe hares (males-maximum 8% (Keith *et al.* 1968), females- only two individuals reported in the literature (Keith & Meslow 1967, Vaughan & Keith 1980)). Both biases would underestimate dispersal distance; thus the emigration frequencies reported here may be an underestimate.

Conclusions

Although my sample sizes are small, a number of conclusions can be drawn from this study. During the increase phase of the hare cycle, emigration of both males and females is common. There is no indication that male-biased dispersal occurs during the increase phase under natural conditions. However, it appears sex-biased natal dispersal may result from higher hare density, possibly as a result of increased social interactions between hares.

Emigrants did not suffer significantly higher mortality rates than philopatric individuals. I did not study any indirect effects of emigration, but the high frequency with which emigration occurs in snowshoe hares may permit such indirect effects to have a significant impact on the population dynamics. It is therefore important that emigration rates and both mortality and reproductive fitness costs of dispersal be established for all phases of the cycle. Such studies may indirectly provide insight into proximate causes of emigration in snowshoe hares. Given the high mortality rate of juvenile hares, small sample sizes will continue to present problems in studying natal dispersal, making it difficult to investigate proximate causes of emigration.

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CHAPTER 2. JUVENILE HARE SURVIVAL

Introduction

Most populations of snowshoe hares (*Lepus americanus*) are cyclic with peak hare densities occurring every 8-11 years (Elton & Nicholson 1942, Keith 1990). Although Hudson Bay fur return records dating back two centuries give indirect evidence for these cycles (Keith 1963), it is only within the last century that researchers have begun studying the demographic changes associated with cycles. The amplitudes of hare cycles that have been studied differ, ranging from ten to one hundred fold density changes from low to peak densities (Meslow & Keith 1968, Keith 1981, Krebs *et al.* 1986, 1995). However, trends in hare survival throughout the cycle are consistent among studies. Survival of both juvenile and adult hares is higher during the increase than the decline phase of the cycle, although changes in survival of juvenile hares are more dramatic (Green & Evans 1940a, 1940b, Windberg & Keith 1976, Keith 1981, Krebs *et al.* 1986). Two studies have found that the single factor most closely correlated with changes in density is juvenile survival until mid-winter (Keith & Windberg 1978, Krebs *et al.* 1986).

Most studies of juvenile hare survival have considered all juveniles born within a summer as equal and estimate the number of juveniles surviving to breed the following year (Green & Evans 1940a, 1940b, Keith 1981, Krebs *et al.* 1986). However, adult snowshoe hares produce up to four litters per season (Cary & Keith 1979). Breeding is synchronous within an area, resulting in distinct and distinguishable litter cohorts, or groups, of juveniles being produced in a summer. Previous studies of survival of pre-weaning (O'Donoghue 1994) and post-weaning hares (Windberg & Keith 1976, Dolbeer & Clark 1975, Boutin 1979) have shown that survival may differ among litter groups. Although such differential survival may not affect the estimates of the number of juvenile hares surviving to reproduce, it may have implications for the population if different litter groups have different reproductive capacities in their first year. Additionally, as the number of litters produced by females may vary

throughout the cycle (Cary & Keith 1979), differential survival among litter groups may be an important component in the reproductive patterns of adult female hares.

There are several reasons why survival may differ among hares from different litter groups during their first year of life. Predation pressure fluctuates through time as availability of alternative prey changes (e.g. adult ground squirrels begin to hibernate by mid-July, T. Karels personal communication), and some predators, like coyotes, cache hares in the fall or early winter in addition to killing hares for immediate consumption (O'Donoghue 1997). As predation pressure changes, hares from different litter groups will be different ages and sizes, which may differentially affect their susceptibility to predation. Additionally, the availability of herbaceous plants, which are the dominant summer foods of hares (Keith 1990), changes as the summer progresses. Food limitation may affect juvenile hares more severely than adults (Windberg & Keith 1976, Keith *et al.* 1984)), possibly because adults are dominant to juveniles (Graf & Sinclair 1987). Similarly, food limitation may affect the litter groups of juveniles differently since older juveniles dominate younger ones (Graf & Sinclair 1987). Presumably, litters born later in the summer will be affected more severely by food limitation than litters born earlier in the summer as a result of this hierarchy.

In this study, conducted during the increase phase of a hare cycle, I determined survival rates of juvenile hares from the age of 5 weeks (weaning) until their first breeding season. I used radio telemetry to determine the fates of dispersing animals and the proximate cause of death of the hares. I examined survival rates for each litter group, all litter groups combined, and adults to determine if survival differed among litter cohorts or between adults and juveniles. I studied hares on control and food addition areas to determine if food addition affected juvenile survival during the early increase phase of the hare cycle.

Methods

Descriptions of the study area, treatments, and hare trapping and collaring procedures are provided in Chapter 1 (general methods). I radio-collared hares from all four litter groups born during 1995 on two treatments (food addition and control) and monitored their survival from June 1995 until April 1996. I classified hares as being from either food addition or control areas based on the grid on which they were collared.

Monitoring of Hares

Each radio-collar contained a mortality switch which caused the pulse rate to double if the collar had not moved in three hours. Hares were monitored from established telemetry locations along the Alaska Highway every one to two days. On each occasion, the hare was recorded as not heard, alive (slow pulse rate), or dead (fast pulse rate). In the spring of 1996, an aerial search of the study area was made for collars that I could not detect from the ground.

When a signal indicated mortality, I located the collar and determined the cause of death (Table 2.1) using signs, such as footprints, feathers, whitewash, scats, marks on the collar, and hare remains at the kill site (F. Doyle, C. Doyle & M. O'Donoghue personal communication). As quantity and quality of kill remains varied, I ranked the certainty of my identification on a scale of 0 to 4, with 4 being definite (Table 2.2). Unless my certainty was 3 or 4, I classified the cause as unknown. If the cause of death could not be determined in the field, I collected the remains for necropsy (Kluane Project 1995). I attributed death to non-predation if the necropsy revealed no bruising, skin punctures, or broken bones and if the hare was found in a typical hare resting spot, such as the base of willow or under deadfall (Dodds 1987, personal observation). Two collars were heard on the fast pulse rate but were not recovered. Since the signals were never heard off the mortality pulse rate, I assumed these two hares had died and classified the cause of death as unknown.

Table 2.1 Classification of causes of death of juvenile hares (Kluane Project 1995). All dominant hare predators found in the study area are represented. During this study, all hare kills could be attributed to one of these causes.

Predation	Other
coyote (<i>Canis latrans</i>)	non-predation
lynx (<i>Lynx canadensis</i>)	unknown
fox (<i>Vulpes vulpes</i>)	shot by hunters
goshawk (<i>Accipiter gentilis</i>)	
great horned owl (<i>Bubo virginianus</i>)	
canid (coyote or fox)	
mammal (lynx, coyote, or fox)	
avian (goshawk or great horned owl)	
unknown predator	

Table 2.2 Description of the probability rating used to indicate certainty of kill identification (Kluane Project 1995).

Probability rating	Description
0	unknown
1	no real evidence of a particular predator but a few suggestions to indicate predator
2	most signs indicate a certain predator but a few inconsistencies
3	nothing to positively identify the predator but all evidence is consistent with one choice of predator
4	known predator (seen at kill, identifiable feather or fur at kill site, distinctive track at kill site)

Unless signs at the kill indicated a more recent time of death, I assumed that hares died the day after they were last heard alive. If the time of death was not known to within two weeks, the hare was censored from the data.

Censoring of Data

Censoring of data refers to the removal of individuals from the study before the study period has ended (i.e. animals that were not followed until their death or the end of the study) (Pyke & Thompson 1986). I censored hares if their collars were removed during the study, if they died from human related activities or were permanently lost, or if the time of death was not known to within two weeks. The censoring date was the day the collar was removed or the day the signal was last heard. The assumption I made in censoring data was that the censoring mechanism (e.g. transmitter failure, dispersal beyond the aerial search area) was not related to the animal's fate (Pollock *et al.* 1989).

Adult Hare Telemetry

Concurrent with my study, adult hare survival was monitored by the Kluane Boreal Forest Ecosystem Project using the same methods (Krebs *et al.* 1992, Kluane Project 1995). In order to compare juvenile and adult hare survival, I analyzed data from collared adult hares on study sites which were used in this study. For adult survival estimates I used only the time period of my study and eliminated 6 juveniles, collared by the Boreal Forest Ecosystem Project in October 1995, from the analysis.

Data Analysis

All 28-day survival estimates were calculated using POLLOCK (Krebs unpublished), a program which performs a Kaplan-Meier estimate and allows for staggered entry of individuals into the study. The Kaplan-Meier procedure allows for censoring of data as the

estimate is based on instantaneous (in this case daily) survival rates during the study period (Pollock *et al.* 1989). I obtained estimates for each age class within each treatment. The age classes I considered were adults, all juveniles combined, litter 1, litter 2, litter 3, and litter 4. I considered groups to be significantly different if their 90% confidence limits (as calculated by Greenwood's standard error (Pollock *et al.* 1989)) did not overlap. I did not analyze the survival of males and females separately as preliminary analysis of my data revealed no effect of sex on juvenile survival. Additionally, previous studies have found no survival difference between sexes at different phases, including the early increase, of the hare cycle (Meslow & Keith 1968, Keith & Windberg 1978, Boutin 1984a, Keith *et al.* 1984, Krebs *et al.* 1986, Boutin & Krebs 1986, O'Donoghue 1994).

Results

Hare Densities

Spring hare densities increased from spring 1994 to spring 1996, indicating that my study took place during the early increase phase of the hare cycle (Figure 2.1). Densities on the food addition grids were approximately double that of control grids during the course of my study (Krebs *et al.* 1995, C.J. Krebs unpublished data).

Telemetry Sample Sizes

I collared 84 individual juveniles (21% of the known and possible juvenile hare population trapped during 1995) and monitored them a total of 10,703 hare days (Table 2.3). One hare day equals one hare collared for one day. During the same time period, 108 adults (69 controls and 39 food hares) were monitored a total of 14,397 hare days.

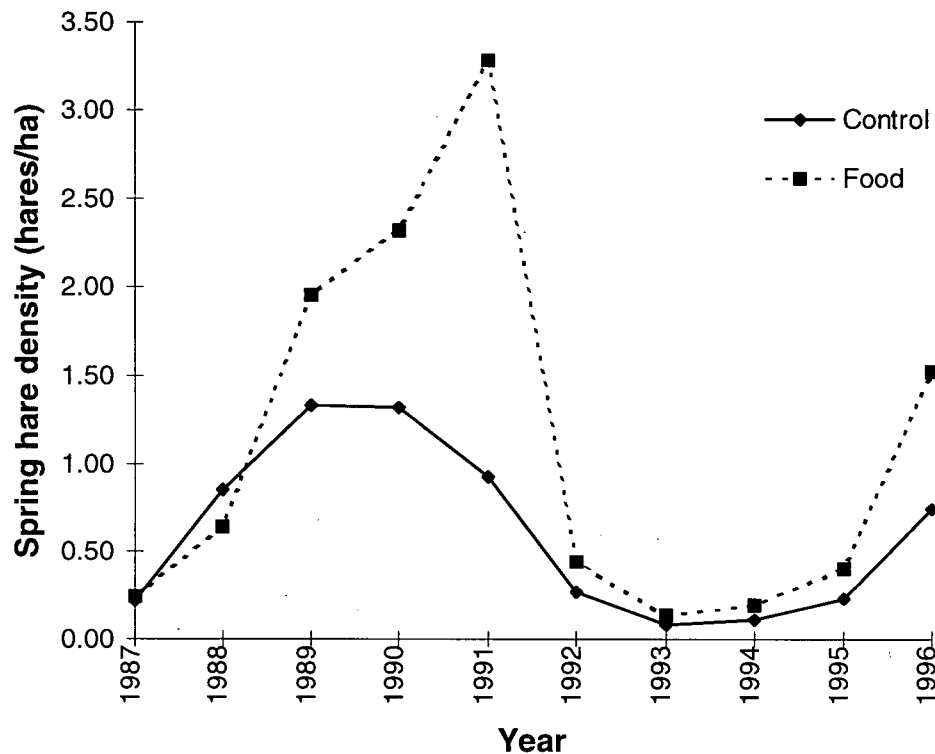


Figure 2.1 Spring hare densities on control and food addition grids (Krebs *et al.* 1995, Krebs unpublished data). Hare densities were estimated using CAPTURE (White *et al.* 1982) and an effective trapping grid area of 60-ha. Control represents average density on control grids 1 and 2 and Food is an average of densities on food addition grids 1 and 2. Spring hare densities on food grids were 1.7 times higher than controls in 1995 and 2.1 times controls in 1996. This study was conducted during the early increase of the hare cycle (June 1995-April 1996).

Table 2.3 Number of individual juvenile hares collared during the study. The number of hare days is indicated in parentheses (one hare day = one hare collared for one day). Of all juveniles trapped in 1995, 29% (48/168) from control areas and 15% (35/232) food addition areas were collared.

Litter	Control	Food	Combined
Litter 1	16 (2,872)	8 (1,324)	23 (4,196)
Litter 2	13 (2,226)	9 (1,392)	22 (3,618)
Litter 3	16 (1,411)	10 (1,103)	26 (2,514)
Litter 4	4 (86)	8 (289)	12 (375)
Total	49 (6,595)	35 (4,108)	84 (10,703)

Survival of Hares

Within each age group (adults and four litters), 28-day survival did not differ significantly between food addition hares and controls (Table 2.4). Therefore, data from the two treatments were pooled for further analyses.

Survival rates did not differ significantly between juveniles (all litters combined) and adults (Figure 2.2). However, when broken down by litter group, fourth litter juveniles had significantly lower survival than adults and first and second litter juveniles, while third litter survival was significantly lower than second litter and adult survival (Figure 2.2).

The 28-day survival differences result from differential survival among age groups during the fall (late August-November) (Figure 2.3). First and second litter survival curves were similar to the adult survival curve, with fairly constant slopes throughout the study. Third litter survival was poor in early fall (August to mid-October), as indicated by the steep negative slope during this time period, after which it became similar to that of older litters and adults. Fourth litter juveniles experienced low survival in late fall (October-November), with only 2 of the 12 collared individuals known to have survived past 11 November 1995.

Causes of Mortality

During the study, 44 hares were known to have died. One was eliminated from the analysis as it was shot by a hunter. Of the remaining 43 hares, predation was the dominant proximate cause of mortality, accounting for 86% (37/43) of the deaths. Non-predation was responsible for only 5% (2/43) of deaths while 9% (4/43) of deaths resulted from unknown causes.

Mammalian predation was constant throughout the study while deaths caused by avian predators contributed little to juvenile mortality rates after October (Figure 2.4 (a)). It also appears that individual predator species, such as lynx, had varying degrees of impact during different seasons (Figure 2.4 (b) and (c), Appendix 5). However, the large number of

Table 2.4 Kaplan-Meier 28-day survival estimates of juvenile and adult hares for the entire study period (June 1995 through March 1996). Survival was not significantly different between treatments within age groups, so individuals from both treatments within each age group were combined in subsequent analyses. "n" refers to the number of animals collared. One hare was only monitored for one week with a baby radio (C. Stefan, unpublished data) and another had its collar removed and was recollared one month later (which the program treats as a new individual), resulting in a different total sample size than that in Table 2.3. Both individuals were third litter juveniles from control areas.

Age Group	n	28-day survival	90% confidence limits
Adults			
Control	71	0.92	0.89-0.94
Food	39	0.96	0.93-0.98
All Juveniles			
Control	51	0.92	0.88-0.94
Food	35	0.91	0.87-0.94
Litter 1			
Control	16	0.93	0.88-0.97
Food	8	0.86	0.00-0.94
Litter 2			
Control	13	0.95	0.90-0.99
Food	9	0.94	0.87-0.99
Litter 3			
Control	18	0.79	0.00-0.86
Food	10	0.90	0.70-0.97
Litter 4			
Control	4	0.44	0.00-0.83
Food	8	0.76	0.00-0.86

Figure 2.2 Kaplan-Meier 28-day survival estimates with 90% confidence limits for juveniles (all litters combined), adults, and each litter group. Sample sizes are provided in parentheses. Juvenile survival (all litters combined) did not differ significantly from that of adults. However, when analyzed by litter, third litter survival was significantly lower than adult and second litter survival, while fourth litter survival was significantly lower than adult, first and second litter survival. The lower confidence limit for fourth litter was 0.000.

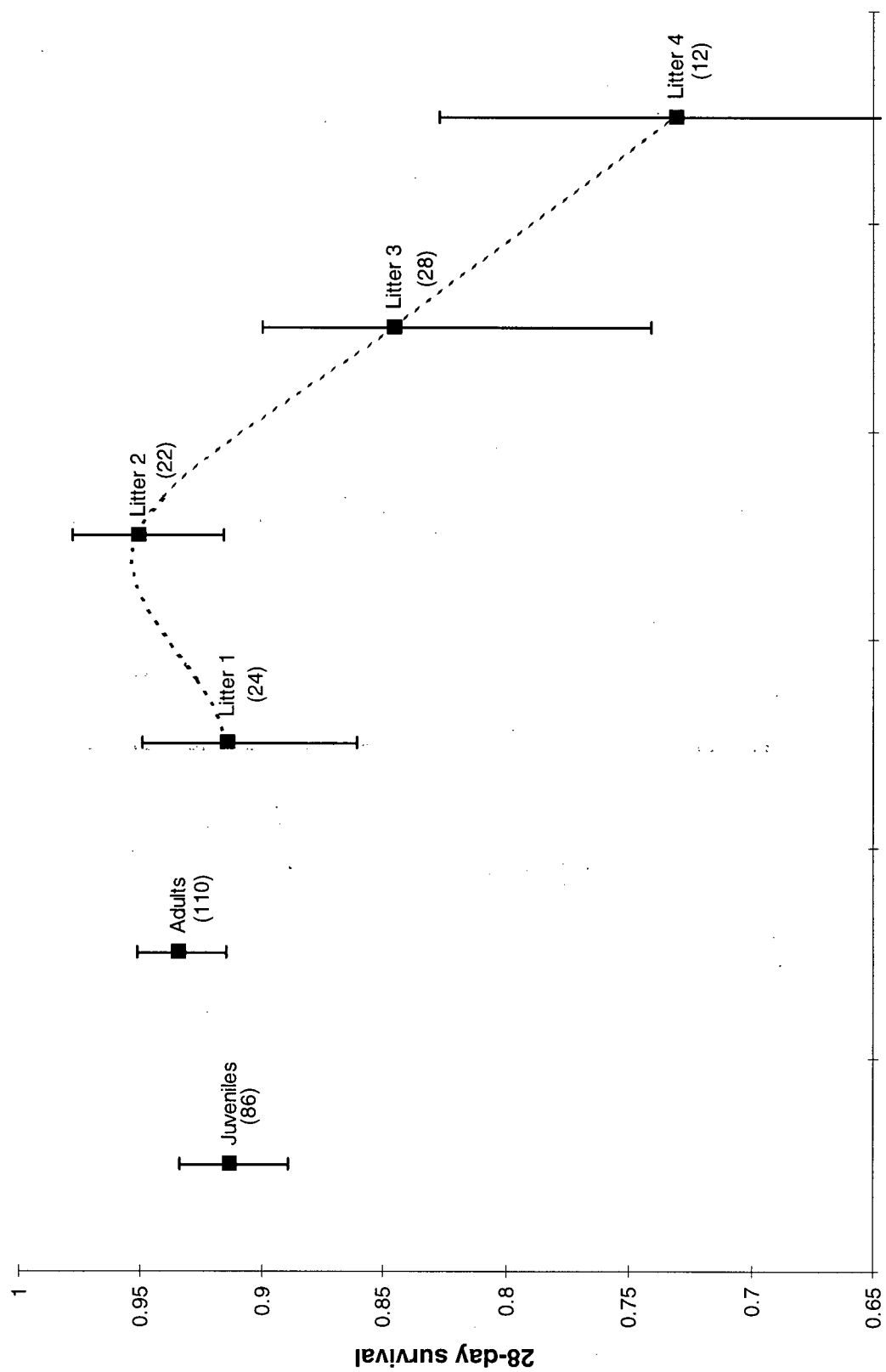


Figure 2.3 Kaplan-Meier survival curves for adults and juvenile litter groups. Adult, first, and second litter survival curves have a fairly constant slope throughout the study period, while the third litter curve has a steep negative slope during early fall, which then levels off to a slope similar to adults and other litters. The fourth litter survival curve has a steep slope during late fall, which then levels off as the two hares that survived until November 11, 1995 also survived the winter. These curves indicate that the differences in survival rates among age groups seen in Figure 2.2 are the result of poor fall survival of third and fourth litter juveniles.

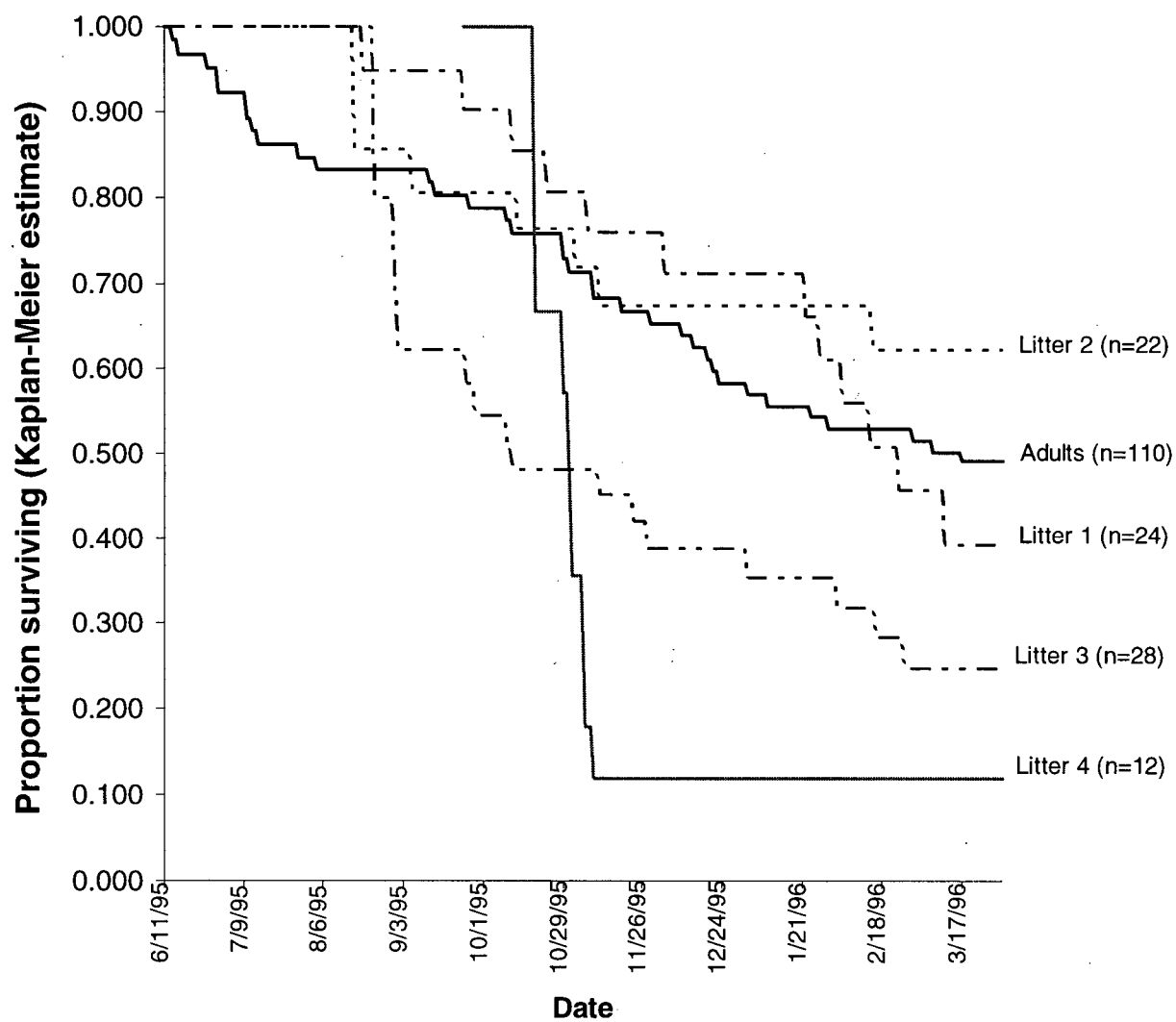
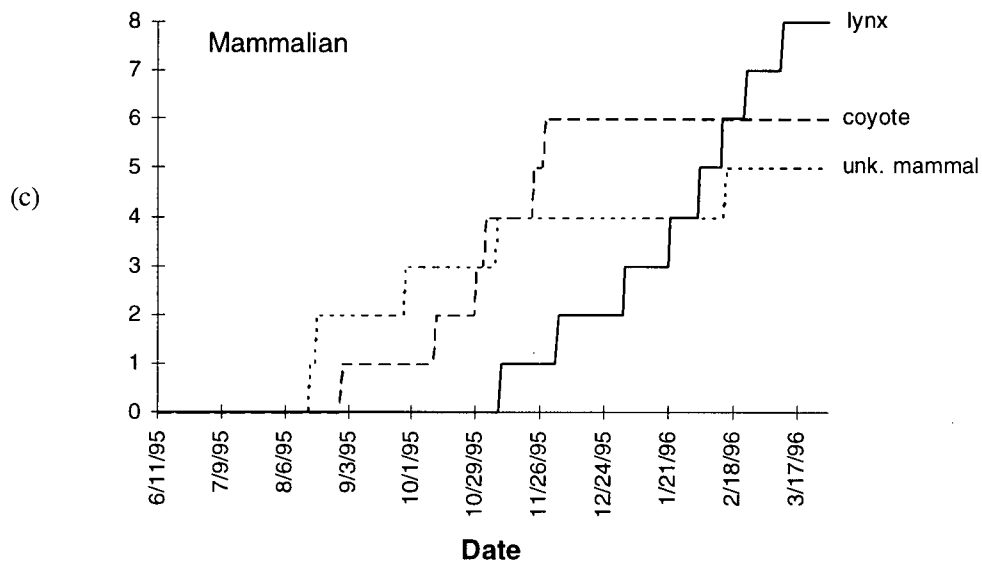
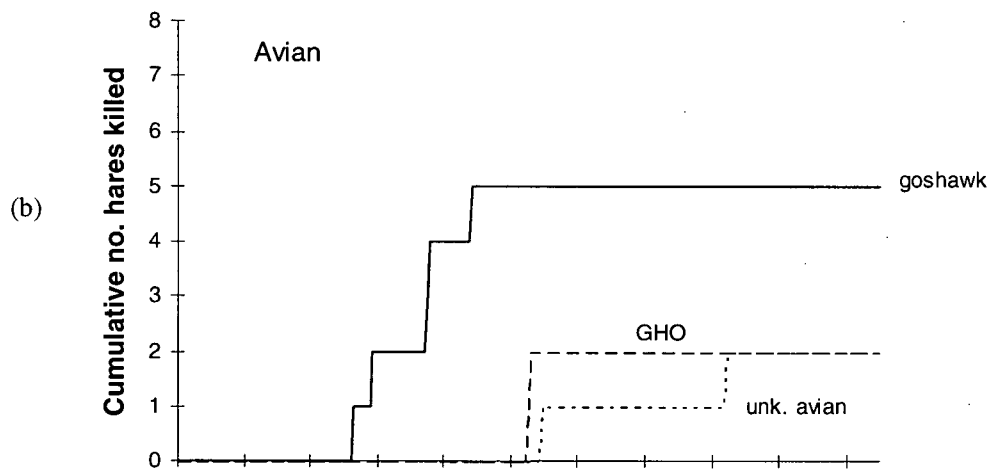
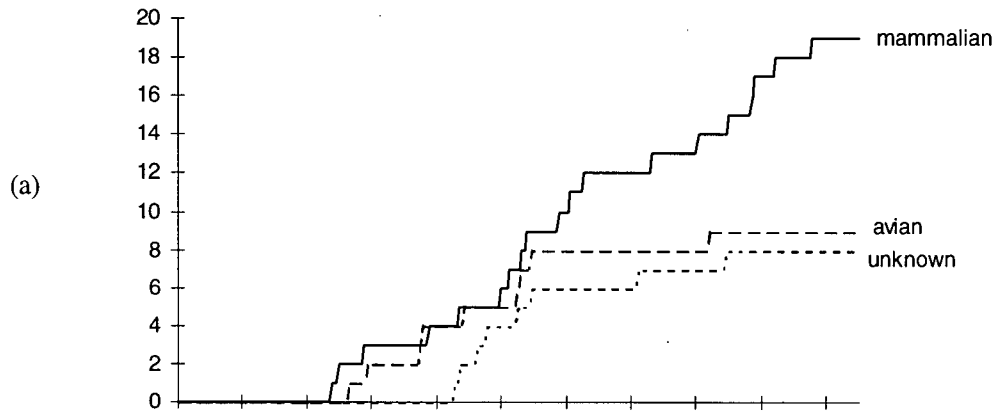


Figure 2.4 Cumulative numbers of radio-collared hares killed by the various classes of predators. GHO stands for great horned owl. No mortality occurred in 1995 between June 11 and 17 August (1,225 hare days). After this time, deaths caused by mammalian predators were fairly constant, while avian predators were responsible for few deaths after mid-October (a). It appears that different species of predators may be responsible for different numbers of kills during different seasons ((c) and (d)). For example, most coyote predation occurred before November, while lynx predation occurred predominantly during winter. However, the large number of kills caused by unknown predators (8 unknown, 2 unknown avian, and 7 unknown mammalian) makes it difficult to draw conclusions.



hares which were killed by unknown predators makes it difficult to draw more precise conclusions.

Discussion

Juvenile Survival

During this study, 28-day survival of juveniles (all litters combined) was high and similar to adults. However, when divided into litter groups, litters born later in the summer (litters 3 and 4) tended to survive less well than adults and juveniles born earlier in the summer (litters 1 and 2), a result of survival differences in the autumn. These post weaning survival differences among juveniles from different litters probably translate into real survival differences among litters since a concurrent study found no difference in pre-weaning (30 day) survival among the first three litters groups (C. Stefan unpublished data).

I assumed that trapping and collaring of hares did not affect their survival. Although collaring may slightly decrease hare survival during the peak and early decline phase of the hare cycle (Keith *et al.* 1984, Boutin *et al.* 1986), a decrease in survival due to collaring has not been detected at any other phase of the cycle, including the increase phase (Brand *et al.* 1975, Boutin & Krebs 1986, Boutin *et al.* 1986). Violating this assumption would cause me to underestimate survival. However, I have no reason to believe that hares from different litters or treatments would be affected differently. Therefore, any bias should be consistent among litters and between treatments and the trends I have documented real.

Most other studies have indicated that juveniles (all litters combined) survive less well than adults during the increase phase of the hare cycle (Keith *et al.* 1968, Keith & Windberg 1978). There are several possible explanations for why I found no difference. The increase phase of the hare cycle lasts for two to four years, and therefore grouping all years of the increase together may obscure changes in juvenile survival within years of the increase phase

(Keith 1981). Such changes in juvenile survival among years of the increase phase do occur. Krebs *et al.* (1995) found similar adult and juvenile survival during the early increase phase (1987), with a dramatic drop in juvenile survival occurring in the late increase phase (1988). The difference between adult and juvenile survival differed significantly by the peak (1989).

It is very difficult to directly compare the survival estimate I obtained to other estimates of juvenile survival in the literature for a variety of reasons. Many are only indices, based on the proportion of juveniles expected in the population (juveniles expected = estimated natality X number of reproductive females) and the actual proportion trapped. Others use trapping data which cannot distinguish between losses due to dispersal and losses due to death, and therefore provide a minimum survival estimate. Since juveniles are more likely to disperse than adults (Keith *et al.* 1984, Boutin *et al.* 1985, Keith 1990), the bias introduced due to dispersal differs between adults and juvenile, making comparisons between these groups problematic. The method I used distinguished between dispersal and death. Four other studies have used telemetry to estimate juvenile survival at different phases of the hare cycle, only three of which have examined post weaning survival (Table 2.5). The survival estimate reported in this study is higher than any of these three. However, I do not know if it is significantly higher since none of the other studies provided confidence limits associated with their estimates.

Seven other studies have examined survival of juveniles on a litter basis (Table 2.6). These studies encompass a wide range of time periods, phases of the cycle, and techniques, some of which provide estimates while others provide only indices. Despite this range, the results are relatively consistent within the six studies that examined juvenile survival to the first breeding season. Five of the six found litter 1 survival > litter 2 survival > litter 3 survival, although none of the authors of the six studies performed any statistical analysis. My results show a similar trend in that I found litters born earlier in the summer survive better

Table 2.5 Survival estimates obtained by telemetry for juvenile snowshoe hares. All post weaning survival estimates are for all litter groups combined.

Age	Time Period ¹	Phase of Cycle	28-day survival ²	Method	Source
Post-weaning	~ 5 wks old - March 31	early increase	0.91 (0.89 - 0.93) ³	Kaplan-Meier	this study
Post-weaning	> 350 g (~ 4 wks old) - May 15	early increase	0.82 ⁴	simple telemetry	Boutin 1979
Post-weaning	15 days - 365 days old	decline	0.87	Trent and Rogstad	Brand <i>et al.</i> 1975
Post-weaning	September - February	decline of a non-cyclic population	0.83	Trent and Rogstad	Keith <i>et al.</i> 1993
Pre-weaning litter 1 litter 2 litter 3	birth - 30 days old	peak	0.48 0.17 0.45	Kaplan-Meier	O'Donoghue 1994

¹ In cases where the time period reported here was subdivided into seasons by the author, I obtained the survival estimate for the time period using the following equation:

$$\text{survival for time period} = \text{survival season 1} \times \text{survival season 2} \dots \times \text{survival season } n$$

² values standardized to 28-day survival by obtaining finite daily survival rate and converting to finite survival rate to 28 days (equation 12.30 in Krebs 1989)

³ 90% confidence limits as calculated by Greenwood's standard error

⁴ assumed monthly survival = 30-day survival

Table 2.6 Summary of results of juvenile hare studies that have reported survival estimates/indices for litter cohorts. Post weaning refers to hares which are trappable (> 3 -4 wks. of age, O'Donoghue and Bergman 1992). "Litters" refers to the litter groups which were examined.

Age	Time period	Phase of Cycle	Litters	Methods	Results	Source
Post-weaning	~ 5 wks old - March 31	early increase	1, 2, 3, 4	telemetry (Kaplan- Meier)	$1 = 2 > 3 = 4^1$	this study
Post-weaning	1st capture - May 1	early increase	1, 2, 3	telemetry (simple), trapping	$1 > 2 > 3$	Boutin 1979
Post-weaning	1st capture - May 1	increase and peak	1, 2, 3	proportion recaptured	$1 > 2 > 3$	Krebs <i>et al.</i> 1986 ²
Post-weaning	1st capture - Nov. or later	decline and increase	1, 2, 3	proportion recaptured	$1 > 2 > 3$	Keith & Windberg 1978
Post-weaning	1st capture - September	peak	1, 2	trapping (min. 28- day survival)	$1 \cong 2$	Boutin 1984b ³
Post-weaning	1st capture -next summer	stable, non-cyclic	1, 2	proportion recaptured	$1 > 2$	Dolbeer & Clark 1975
Pre- and post-weaning	birth - Oct. 28	peak	1, 2, 3	est. age ratio vs. proportion trapped	$1 > 2 > 3^4$	Windberg & Keith 1976
Pre-weaning	birth - 30 days old	peak	1, 2, 3	telemetry (Kaplan- Meier)	$1 = 3 > 2^5$	O'Donoghue 1994

¹ statistically significant differences ($\alpha 0.10$)

² includes data from Boutin 1979

³ does not include results from manipulated areas

⁴ data from experimental manipulation (artificially high density)

⁵ statistically significant differences ($\alpha 0.05$)

than those born later (after mid-July). In 1995, the pre-weaning survival among the first three litter groups was not different (C. Stefan, unpublished data). However, this may not always be the case. At a cyclic peak, second litter juveniles had lower pre-weaning survival than first and second litter juveniles (Table 2.5, O'Donoghue 1994). Because differential survival among litters may occur both pre- and post- weaning and because survival trends among litters may differ between these two age classes, it is necessary to examine both when investigating trends in differential survival among litter groups from birth until sexual maturity.

The high mortality of juvenile hares I observed in the autumn has been reported in two other studies, both of which compared juvenile survival in autumn and winter (Keith & Windberg 1978, Krebs *et al.* 1986). However, in a radio telemetry study conducted during the early increase phase of the hare cycle, Boutin (1979) reported slightly lower survival from December to May than September to December. It is difficult to determine if this result conflicts with mine or is an artifact of the analysis. By dividing the study period into arbitrary time intervals the true results may be obscured. For example, when I analyze my data by seasons (June-August, September-October, October-March), I find no difference among the seasons, even though it is obvious from Figure 2.3 that mortality varies seasonally in an important way. Additionally, Boutin only collared hares > 750 g in late August. It is therefore most likely that the majority of the hares collared were from litters 1 and 2, the two litters which I found had consistent survival throughout the fall and winter.

Juvenile survival in several different species of birds and mammals is related to date of birth. The relationship between survival and season/date of birth can be examined on at least two scales- within a litter and among litters. In general, it would appear that within a given litter group or in animals which have only one cohort of young per year, those individuals born or hatched earlier in the season tend to have higher survival than those born later in the season. This trend has been demonstrated for Marsh Tits (Nilsson & Smith 1988), snow geese (Cooke *et al.* 1984), Manx Shearwaters (Perrins 1966), European Coots (Brinkhof 1995), and red squirrels (O'Donoghue & Boutin 1995). However, in snowshoe hares at the

peak of the hare cycle, those individuals within a litter group which were born closer to the mean parturition date for each litter cohort survived better than those born further from the mean in either direction (O'Donoghue & Boutin 1995). O'Donoghue & Boutin (1995) attribute the difference between red squirrels and snowshoe hares to different selection pressures. Predation is a major influence affecting early juvenile survival of hares but not red squirrels because red squirrels do not emerge from their natal nest during their first weeks of life and therefore are unavailable to most predators until emergence at approximately 50 days old (Larsen & Boutin 1994, O'Donoghue & Boutin 1995). The predator swamping hypothesis (Darling 1938, Ims 1990) would therefore predict that it would be advantageous for hares to be born near the mean parturition date. For red squirrels, other factors, such as competitive ability, may determine play a more important role in influencing the impact of date of birth on survival.

For multi-littered and multi-brooded species, there is also a trend for those litters born earlier in the summer to have higher survival or recruitment rates than those born later in the summer. In song sparrows, young from the second brood hatched in the season have a lower probability of being recruited into the breeding population than those from the first brood (Hochachka 1990). For white-footed mice, the life expectancy of litters born in the spring is greater than nine weeks, while those born in the fall have a life expectancy of less than three weeks (Goundie & Vessey 1986). However, in wood mice, litters born in the middle of the breeding season may have the highest survival (Halle 1993). In grey squirrels, there is no difference in survival between spring-born and summer-born litters (Thompson 1978). Litter cohorts of grey squirrels differ from hares and other species cited here in that the interval between the litter groups is quite long (114 days).

There are several reasons individuals born earlier may have a survival advantage over later born individuals. Those born early may be dominant over those born later, which may provide a survival advantage in some social systems. For example, Marsh Tits born earlier become established in winter flocks and obtain dominance earlier (Nilsson & Smith 1988).

Tinbergen *et al.* (1985) found yearly survival differences among Great Tits could be explained by over winter seed availability for first brood individuals, but second brood survival was influenced by both seed availability and first brood density, with survival being negatively correlated with first brood. They suggest competition between the two broods before winter causes the negative correlation, and that the age difference between first and second broods gives the first brood a survival advantage. As well as establishing a situation in which asymmetric competition can take place, production of several broods each year also means young animals will be different ages and sizes when interacting with a similar environment. The possibility that age may influence survival as predation pressure fluctuates will be discussed later to explain the results found in this study.

Although there appears to be overwhelming evidence that individuals born early in the season have higher survival over the time intervals they have been studied, it is important to note that with the exception of O'Donoghue & Boutin (1995), the examples cited here are all based on ring recoveries of birds or recaptures of animals. Such techniques may artificially inflate the differences in species in which dispersal is season dependent. In such species individuals, born earlier in the summer live in their natal area longer and may have higher site fidelity and therefore are more likely to be resighted (Cooke and Abraham 1980 *in* Cooke *et al.* 1984). Within a litter or brood, some of the difference in juvenile survival may be associated with parent quality rather than time per se. For instance, in European coots poorer parents reproduce later in the season (Brinkhof 1995). Additionally, because the proportion surviving to breed depends on both the monthly survival and the number of months from birth to first breeding season, individuals born early may have a lower survival to breeding even when they have higher instantaneous survival. In this study first litter juveniles bred for the first time when they were 9-10 months old, while those from fourth litter bred when they were approximately six months old. Nevertheless, juveniles born earlier in the season survived significantly better than those born later, regardless of whether 28-day survival or survival until breeding was considered (Figure 2.3).

The Role of Predators

Predation was the main proximate cause of death in radio-collared juvenile hares in this study. Similarly, previous studies of adult hares have found that predation accounts for the majority of hare deaths at all phases (Keith *et al.* 1984, Boutin *et al.* 1986, Trostel *et al.* 1987, Krebs *et al.* 1992, 1995, Murray *et al.* 1997). In this study, third litter juveniles survived at a rate similar to adults and juveniles from first and second litters after early September, while fourth litter juvenile survival dropped dramatically at this time (Figure 2.3). As predation is the main proximate source of mortality, these results suggest that predators may be taking advantage of an easy prey (Mykytowycz *et al.* 1959, Donázar & Ceballos 1989, Rohner & Krebs 1996). Predators may also prefer a certain sized prey, which may not be related to age or inexperience. For example, goshawks at Kluane kill juvenile hares which average 698g ($n = 25$, std. err. = 56, F. Doyle unpublished data) although the hares available to goshawks range from newborns (approximately 75g, C. Stefan unpublished data) to adults (1500g, O'Donoghue 1997). As juvenile hares grow, they may pass through a "window" in which they represent the preferred prey size or easiest prey to catch, which may explain the apparent "switching" of predator focus from third to fourth litter hares.

Due to the large number of kills for which I could not determine the species of predator, I can conclude little about the role of specific predators. There do appear to be some general trends, however. Although mammalian predation stays fairly constant during the fall and winter, lynx and coyotes show different seasonal patterns that are related to hunting strategies (Murray & Boutin 1991, O'Donoghue 1997). Coyote predation occurs primarily in the fall, even if coyotes account for all the kills by unknown mammals. Coyotes do not travel efficiently in deep snow and tend to cache hares in the autumn for the winter. Lynx, which have long legs and large paws making them well adapted for hunting in deep snow, killed juveniles throughout the study.

Unlike mammalian predation, avian predation was not common after October (this trend exists even if I assume all unknown predators are avian). Since the dominant avian

predators of the system, goshawks and great horned owls, are both residents, the drop in avian predation after October was unexpected. The overall density of avian predators may have dropped if young of the year dispersed from the area, but such dispersal was not examined. Also, fledglings may have lost fewer of their kills to scavenging as they became more experienced predators, reducing the number of hares they had to kill for food (F. Doyle, personal communication).

What can explain the differential mortality among litters?

Neither age nor season in isolation is associated with the higher mortality rates observed in the later litters. This conclusion can be reached by comparing survival of litters 1) at the same age and 2) at the same time (e.g. fall). Both age-specific and season-specific survival of third and fourth litters are much lower than in first and second litter at the time of high juvenile mortality (September-November). Similarly, Windberg & Keith (1976) reported "both time- and age-specific differences" in survival among litters at an artificially high population density. This trend can be explained if different litters face different stresses at the same age or if the same stress has different effects on the various litter groups at a given point in time. There are reasons to expect that both of these situations occurred in this study.

The stresses faced by juvenile hares that may increase susceptibility to predators, directly or indirectly, can be divided into two categories: 1) age dependent stresses such as weaning, growth, predation pressure due to size or experience and 2) season dependent stresses, such as diet shifts, habitat changes, predation pressure changes due to alternative prey availability, predator energy requirements or density of predators. The impact of both types of stress on survival may vary depending on the date of birth. For example, juveniles from first and second litters have access to herbs and forbs during the weaning period, but third and fourth litter juveniles are weaned to less nutritious browse. At the time of fall molt, first and second litter hares are adult weight, while third and fourth litters are still growing (Keith *et al.* 1968, O'Donoghue and Krebs 1992, personal observation). Both low weight and

poor food quality may result in increased foraging by juveniles from third and fourth litters relative to those from first and second litters in the fall. Increased movement is associated with a decrease in hare survival (Sievert & Keith 1985).

Predation pressure varies over time for all litter groups for many reasons, such as caching of hares by coyotes in the fall and changes in the availability of alternative prey species. As evidence of fluctuating predation pressure, all collared juvenile hares survived until mid-August. The first juvenile hare deaths coincided with the hibernation of juvenile ground squirrels (T. Karels, personal communication), which suggests that some predators may have shifted from ground squirrels to hares as food. Even though such changes in predation pressure will affect all hares, cohorts that are "easier prey" due to their inexperience or activity rate may be killed disproportionately. Predator choice may serve to augment age dependent differences in survival due to stress.

Why did food addition have no observable impact on survival?

Although third and fourth litter survival tended to be lower on control grids than in food addition areas, this trend was not significant. If this trend could be shown to exist, it would indicate that low food availability may have reduced survival of later litters and perhaps that weaning is more stressful in late summer. However, closer inspection of the data does not support a role for food in improving third and fourth litter survival. The confidence limits associated with these estimates are very large and sample sizes are small. Most importantly, Kaplan-Meier plots of survival of hares from food and control areas show no consistent trends; sometimes hares from food addition areas survive better than controls and at other times the reverse is true (Appendix 6). More convincing trends over more years would be necessary to argue for a positive effect of food on juvenile hare survival during the early increase phase of the hare cycle.

There are several explanations why the food addition treatment did not noticeably increase juvenile hare survival. A positive effect of food addition on survival may have gone

undetected because some of the juveniles collared on food addition areas dispersed off the treatment. Since food addition also increased hare density, an improvement in body condition and survival could have been offset by increased predation pressure because predators focus on areas of high hare densities (O'Donoghue 1997). Although the predator effect should lag behind the body condition effect, my coarse methods would not detect a lag and I would conclude there was no effect at all. However, a more probable explanation is that food is not limiting during the increase phase of the hare cycle. In a hare cycle in Alberta, hares had more overwinter food available than required except during the decline phase of the cycle (Table 7 in Keith 1990). At Kluane, adult male body condition did not differ on food addition and control areas in October 1995 (Appendix 4), and diet quality on food areas, as measured by protein and fiber intake and fiber content of turds, was not higher on food addition treatments (K. Hodges, unpublished data). Additionally, all hares from control areas for which cause of death was known died from predation, which suggests they were not starving to death. However, this final point may be complicated if food stress lowers survival by increasing the risk of predation. Under this scenario, predation may be the proximate cause of death, but it is merely a substitution for hares which would have died due to starvation eventually anyway (Keith *et al.* 1984, Sievert & Keith 1985).

The effect of food limitation has been tested experimentally in two ways. The first is by examining hare survival when food is limited through experimental manipulation. Studies of this kind have shown that food limitation decreases both adult (Vaughan & Keith 1981) and juvenile (Windberg & Keith 1976, Vaughan & Keith 1981) hare survival, more so for juveniles than adults (Windberg & Keith 1976, Vaughan & Keith 1981). The second method is to provide food to a population and measure survival (reviewed by Boutin 1990). Food addition appears to increase hare survival in peak or declining populations (Boutin 1984a, Boutin *et al.* 1986, Krebs *et al.* 1995, Murray *et al.* 1997) when food may be limiting (Table 7 in Keith 1990) but not during other phases of the hare cycle (Krebs *et al.* 1995, Boutin *et al.* 1986) when natural food is not limiting. Overall, these results suggest that food addition will

increase survival in populations where food limitation is occurring. Thus, it is not surprising that I detected no effects of food addition on survival during the early increase when food is not limiting. In contrast, Krebs *et al.* (1986) found food addition increased survival (estimated by recapture data) relative to controls during the increase and peak phase, yet decreased survival in the decline phase due to predator concentration in the decline. It is possible that this discrepancy is due to the addition of food in late winter only or by hares dispersing out of the higher density populations on the food addition areas.

Conclusions

I conclude from this study that survival is unequal among the different litter groups of juveniles produced in a summer during the increase phase of the hare cycle at Kluane, Yukon Territory. Assuming these results can be extrapolated to other cyclic populations of snowshoe hares, this conclusion has potential implications for survival estimates, theoretical models of hare population cycles, and reproductive strategies of snowshoe hares.

Most estimates of juvenile survival have combined all litter groups, assuming that they survive equally following weaning. This study shows that litter groups can have significantly different survival rates. Furthermore, the survival estimate for all litters combined was not an average of the litter survival of the four litters because hares from early litters (one and two) were collared in greater numbers and for a longer time than were later litters (three and four). They contributed disproportionately to the overall survival estimate and artificially inflated the value. Unless the juveniles included in a study represent true proportions of individuals from the different litter groups in the population, survival estimates may be biased by an unknown amount and in an unknown direction. Future studies need to examine juvenile survival on a litter basis when possible to ensure that such biases are avoided.

Some theoretical models of hare cycles have used estimates of juvenile survival (all litters combined) and average reproductive output. As both survival and adult reproductive

output vary among litter groups within a summer, the use of overall values may yield erroneous results. Future models should investigate the sensitivity of results to the use of overall survival and reproduction versus survival and reproduction on a litter basis.

Hares in the Yukon produce from two to four litters of young season at various stages of the cycle (C.J. Krebs unpublished data). The low survival of fourth litter juveniles raises the question of why females would invest in this litter, as it presumably has some cost. To answer such questions, data for pre- and post-weaning survival of each litter is required. These potential fitness benefits then need to be compared to any detriment in terms of future reproduction suffered by females who produce a fourth litter (Stearns 1992). Additionally, some of the reproductive changes seen though the hare cycle could be attributed to differential survival among litters if the litter groups have varying reproductive potential in their first breeding season.

In this study, the differential mortality seen among litters resulted from a two month period of differential survival in the fall. It appears that fall may be the crucial time period for juvenile hares during the increase phase of the hare cycle, and future studies should attempt to determine if this is consistent throughout the hare cycle.

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GENERAL CONCLUSIONS

This study failed to support numerous expectations about dispersal and survival of juvenile snowshoe hares. First, emigration of juveniles was unexpectedly high (Chapter 2). Although it was previously known that juveniles disperse more often than adults (Windberg & Keith 1976, Keith *et al.* 1984, Boutin *et al.* 1985), the emigration frequency of 50% is the highest value reported for snowshoe hares. It is possible the value is high because emigration is more common during the increase phase of the hare cycle than during the other phases of the cycle in which juvenile dispersal has been studied. Yet using indirect methods, it has been shown that hare dispersal rates are highest during the peak and early decline phase of the hare cycle (Windberg & Keith 1976, Boutin *et al.* 1985). However, the dispersal rates reported are much lower than the emigration rate I have reported. Dispersal rates in *Microtus* spp. are highest during the increase phase of the vole cycle (Myers & Krebs 1971, Krebs *et al.* 1976). To determine if this is also the case in snowshoe hares, emigration rates will have to be obtained using radio telemetry at the different phases of the cycle.

Male-biased dispersal did not occur on control areas, but did occur on the higher density food grids. For reasons stated in Chapter 1, this difference may be the result of the increased hare density on the food areas. This result is consistent with previous dispersal studies in hares which indicate that sex-biased dispersal does not occur in snowshoe hares (Windberg & Keith 1976, Boutin 1979, 1984a) except at high densities (O'Donoghue & Bergman 1992). Results of this study support the hypothesis that social interactions may play a role in hare dispersal, either as a proximate cause to emigration or by influencing the ease with which a hare is able to immigrate into a new population (Boutin 1984a, 1984b, Graf & Sinclair 1987).

A common assumption in the dispersal literature is that dispersers suffer a higher mortality rate than those individuals which are philopatric. I found this assumption was not supported for juvenile hares at the increase phase of the cycle. Hares have a very different life

history and social system than those species in which dispersal was found to have a high mortality cost. They do not defend a territory, naturally have high movement rates even when not dispersing (K. Hodges unpublished data), and do not rely upon structures such as burrows for protection from predators. It is therefore likely that the action of dispersing long distances probably does not increase their risk of predation to the same extent that it does in other species, such as ground squirrels. There is increasing evidence that the assumption that dispersal equals death is not valid for all species, and differences between taxa must be considered before evidence for this assumption is universally applied. In snowshoe hares during the increase phase of the hare cycle, the high survival of emigrants may allow individuals to colonize habitats and areas that were vacant during the low of the hare cycle (Wolff 1980, 1981).

The high emigration rate of juveniles and the fact that these emigrants did not suffer higher mortality has implications for juvenile hare survival studies which have relied upon recapture data to obtain survival rates. In this study, approximately 25% of juveniles that disappeared from the study grids had emigrated and survived to the end of the study period. Recapture methods would have assumed these animals had died. If emigration rates vary throughout the cycle, the survival trends through the cycle reported in such studies may be partially due to changes in dispersal. For example, the decrease in survival of juveniles during the late increase phase of the cycle found by Krebs *et al.* (1995) may simply be due to increased dispersal during the late increase phase of the cycle.

This study has shown that in terms of survival during the increase phase of the hare cycle, all litter groups are not equal (Chapter 2). One of the questions which remains to be answered is how this may affect the reproductive strategies of female hares during the hare cycle. For example, in this study, very few (2 of 12) fourth litter juveniles survived to reproductive age. Given such a low survival rate, why did the females invest in this litter as presumably there was some cost associated with its production?

The results presented in this thesis indicate that in future studies, it is important to recognize that juveniles born at different times during the summer may survive differently. It is important to establish whether these differences impact the numerical and survival trends that are measured. Simulation models to test the sensitivity of estimates to differential survival among litters may provide a useful tool. Even if such simulations indicate survival estimates are robust to the survival differences among litters, they should not be dismissed as unimportant. At some phases of the hare cycle, yearlings make up the majority of the population (Green & Evans 1940, Cary & Keith 1979). Litter differences may be important when attempting to explain qualitative differences in populations at different phases of the cycle and among individuals.

Based on the results from this study, I recommend future studies address three critical questions:

- (a) What is the natal dispersal rate during the peak and decline phase of the hare cycle?
- (b) Are there any reproductive or long term survival benefits to natal dispersal?
- (c) Does the time of year a female is born (i.e. litter group) affect her reproductive capabilities in her first breeding season?

If these question could be answered, they would help determine if the high natal dispersal rates and the differential survival among litter groups observed in this study play a role in the hare cycles we observe.

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APPENDICES

Appendix 1 Mean date of birth for each litter group on each grid in 1995 (C. Stefan unpublished data).

Litter	Control 1	Control 2	Control 3	Food 1	Food 2
1	May 15	May 25	May 25	May 11	May 15
2	June 21	June 18	June 23	June 17 ¹	June 9
3	July 29	July 27	July 28	July 20	July 20

¹ estimated using a gestation period of 36 days

Appendix 2 Minimum distance required to be classified as an emigrant (2 adult home range diameters). Home range size was calculated using 95% minimum convex polygon based on a minimum of 12 telemetry locations collected during the summer of 1995 (CALHOME, Kie *et al.* 1994), and home ranges were assumed to be circular for the calculation of home range diameters. There was no difference in adult home range size between food addition and control areas, however female home ranges were significantly smaller than those of males (K. Hodges, unpublished data). Means are reported as mean of control and food addition hares combined \pm standard deviation.

Sex	n	Home range size (ha)	Home range diameter (m)	Minimum dispersal distance required to be classified as an emigrant (m)
Male	12	12.97 \pm 5.07	406	812
Female	23	6.04 \pm 4.11	277	554

Appendix 3 Dispersal distances and fates for radio-collared juveniles whose nest site location was known or could be determined.

Tag	Treatment	Sex	Litter	Dispersal Distance (m)	Emigrant?	Emigration Date	Emigration Age (days)	Fate ¹	Date of Death
B1685	control	F	1	20	no			1	
B722	food	F	2	70	no			1	
B6977	food	F	3	170	no			1	
B7702	control	F	3	360	no			2	Feb. 3
B1687	control	M	1	330	no	July 26 ²	62	1	
B1311	control	M	2	130	no			1	
B1318	control	M	2	420	no			1	
B1320	control	M	2	430	no			1	
B7839	food	M	3	260	no			1	
B1457	control	M	3	90	no			3	Oct. 11
B764	control	M	3	400	no			3	Sept. 1
B7744	control	M	3	540	no			3	Nov. 28
B1347	food	F	2	60	no			3	Aug. 17
B1456	control	F	3	350	no			3	Oct. 9
B1636	control	F	3	200	no			3	Sept. 25
B1647	control	F	3	350	no			3	Sept. 28
B755	food	F	3	250	no			3	Aug. 31
B762	control	M	2	210	no			3	Oct. 13
B1375	control	M	1	2540	yes	June 25	31	1	
B1683	control	M	1	950	yes	June 27	40	1	
B1686	food	M	1	2650	yes	June 29	45	3	Jan. 27
B1682	food	F	1	1560	yes	July 3	49	3	Nov. 7
B1698	food	M	1	1750	yes	July 6	52	2	Feb. 24

Appendix 3 Continued

Tag	Treatment	Sex	Litter	Dispersal Distance (m)	Emigrant?	Emigration Date	Emigration Age (days)	Fate ¹	Date of Death
B1260	food	M	1	2610	yes	July 15	61	2	March 11
B1535	control	M	2	1250	yes	July 27	39	2	Feb. 15
B1533	control	M	2	1200	yes	July 27	39	3	Aug. 17
B1310	control	F	2	1460	yes	July 28	39	1	
B720	food	M	2	2070	yes	July 31	52	1	
B1307	food	F	3	600	yes	Aug. 2-Aug. 22	13-33	3	Aug. 24
B1638	control	M	3	6850	yes	Aug. 12	140	2	Feb. 16
B1648	food	F	3	2180	yes	Aug. 27	40	3	Nov. 11
B1473	control	M	3	1090	yes	Oct. 12-Nov. 23	83-125	3	Nov. 23
B1329	control	F	1	660	yes	Oct. 13-Jan. 22	146-247	3	Jan. 22
B773	control	F	3	16730	yes	Oct. 27	89	1	
B1640	control	M	3	>900m	yes	Nov. 12	105	3	Feb. 2

¹ Fate 1 = alive until April 1, 1996; Fate 2 = died between February and April, 1996; Fate 3 = died before February 1, 1996. Hares with fates 1 or 2 were used in the natal dispersal distance analysis, all hares were used in the survival cost of emigration analysis, and all emigrants were included in the age/date of emigration analysis.

² This individual emigrated 910 m and then returned to its natal area 62 days later. He was classified as a non-emigrant for the natal dispersal distance and cost of dispersal analyses but included as an emigrant in the age/date of dispersal analysis.

Appendix 4 Indices of body condition for adult male hares trapped on control and food addition treatments during October, 1995. Condition is expressed as mean \pm standard deviation. No difference between food addition and control areas was detected.

Index ¹	Control	Food	t - value ²	df	p - value (2-tail)
n	10	7			
Condition 1	8.677 \pm 0.185	8.580 \pm 0.099	1.40	14.3	0.18
Condition 2	1.011 \pm 0.061	0.987 \pm 0.030	1.10	13.9	0.29

¹ Condition 1 was calculated as in Bailey (1968) and Hearn *et al.* (1987) using
condition = (weight ^{1/3} / length of right hind foot) X 100.

This index has been recently criticized by Krebs & Singleton (1993), so I calculated an alternate condition index (Condition 2). A power curve was fitted to all weight and right hind foot values of adult males trapped in October 1995 using the NONLIN module in SYSTAT (O'Donoghue & Krebs 1992, Krebs & Singleton 1993). The resulting relationship was

$$\text{weight} = (\text{right hind foot length})^{1.57} - 653 \text{ g.}$$

Using this relationship, the expected weight of all individuals was calculated based on right hind foot length. Condition 2 is the ratio of observed weight to expected weight.

² Since variances were not equal between the groups, the *t*-test was performed using separate variances.

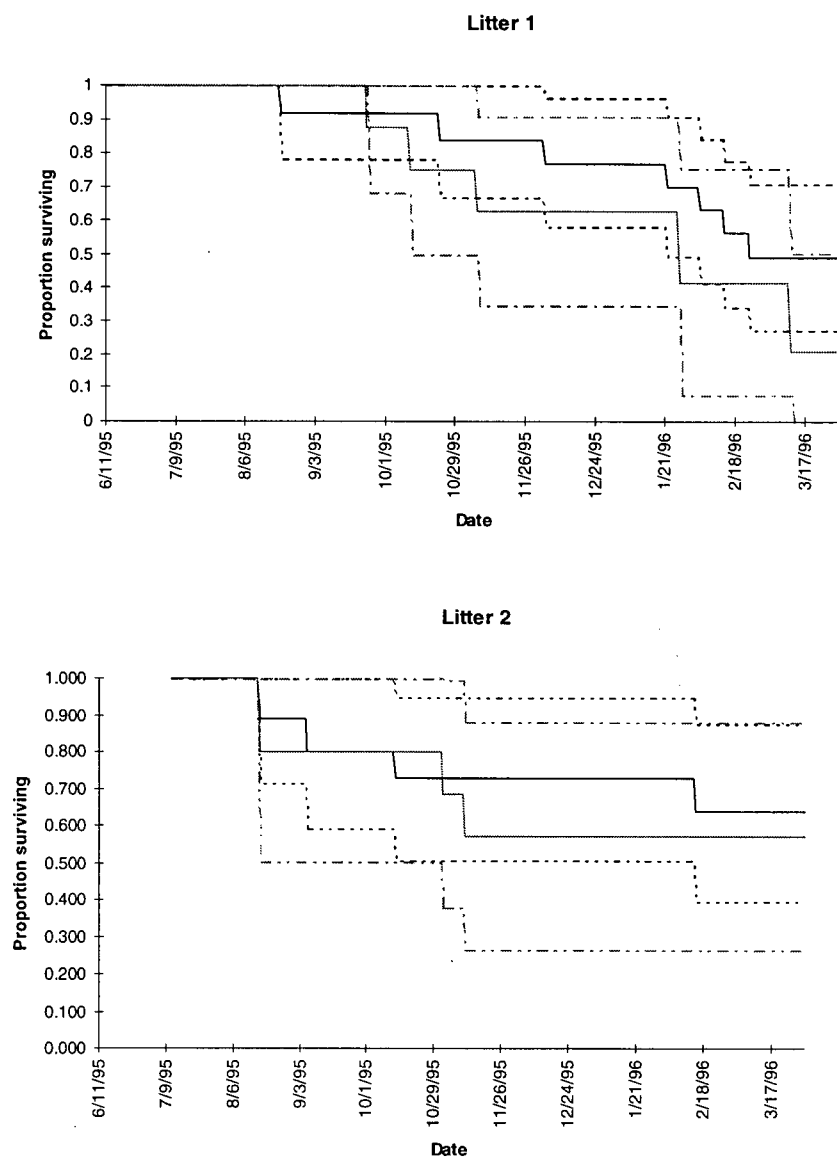
Appendix 5 Date and cause of death of radio-collared juveniles that died between June 1995 and April 1996. All "suspected fates" had an identification certainty of 2 (Table 2.2). GHO stands for great horned owl.

Tag	Treatment	Sex	Litter	Date Killed	Age Killed	Known Fate	Suspected Fate
B755	food	F	3	31/8/95	43	coyote	
B1350	food	M	1	11/10/95	155	coyote	
B7892	food	F	4	29/10/95	66	coyote	
B757	food	M	2	2/11/95	145	coyote	
B1473	control	M	3	23/11/95	126	coyote	
B7744	control	M	3	28/11/95	131	coyote	
B7716	food	F	4	9/11/95	69	lynx	
B1639	control	F	1	4/12/95	195	lynx	
B1629	control	M	3	2/1/96	235	lynx	
B1329	control	F	1	22/1/96	247	lynx	
B1549	control	M	1	4/2/96	256	lynx	
B1546	control	M	1	14/2/96	266	lynx	
B1698	control	M	1	24/2/96	290	lynx	
B1260	food	M	1	11/3/96	306	lynx	
B1307	food	F	3	24/8/95	36	goshawk	
B764	control	M	3	1/9/95	34	goshawk	
B1680	food	M	1	24/9/95	138	goshawk	
B1636	control	F	3	25/9/95	67	goshawk	
B762	control	M	2	13/10/95	118	goshawk	
B2318	food	F	4	5/11/95	73	GHO	
B8462	food	M	4	6/11/95	74	GHO	
B1547	control	F	1	20/8/95	89	canid	
B1533	control	M	2	17/8/95	61	mammal	
B1647	control	F	3	28/9/95	61	mammal	lynx
B1682	food	F	1	7/11/95	177	mammal	lynx
B1535	control	M	2	15/2/96	242	mammal	lynx
B1306	food	F	2	11/11/95	154	avian	goshawk
B1686	food	M	1	27/1/96	257	avian	GHO
B1305	control	F	2	6/9/95	79	unk. pred.	
B1457	control	M	3	11/10/95	78	unk. pred.	
B1475	control	M	4	19/10/95	48	unk. pred.	mammal
B1536	control	F	1	23/10/95	153	unk. pred.	mammal
B7021	food	M	4	5/11/95	73	unk. pred.	
B1648	food	F	3	11/11/95	117	unk. pred.	

Appendix 5 Continued

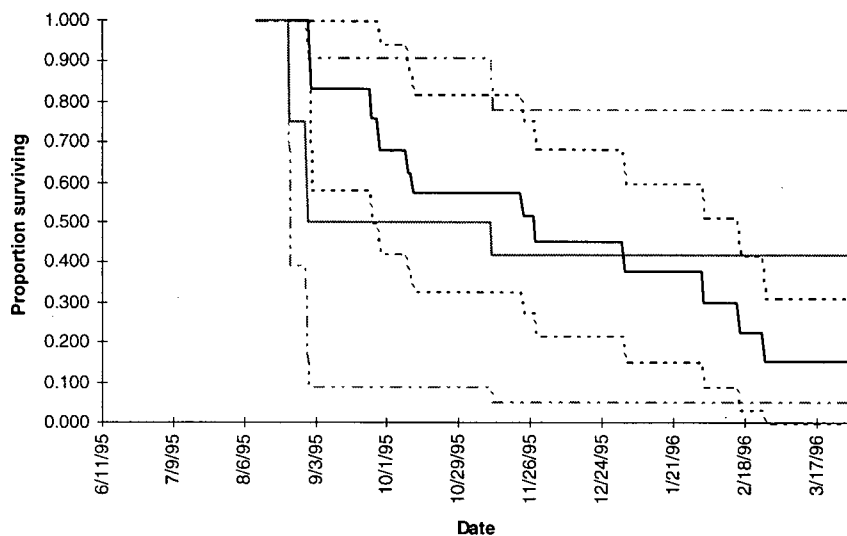
Tag	Treatment	Sex	Litter	Date Killed	Age Killed	Known Fate	Suspected Fate
B1626	control	F	3	27/12/95	230	unk. pred.	
B7702	control	F	3	3/2/96	185	unk. pred.	mammal
B1493	control	F	2	2/4/96	287	unk. pred.	lynx
B1649	food	F	3	11/10/95	82	shot	
B1347	food	F	2	17/8/95	68	non-pred.	
B7834	food	F	4	1/11/95	69	non-pred.	
B1456	control	F	3	9/10/95	76	unknown	
B1455	control	F	4	31/10/95	60	unknown	
B1640	control	M	3	2/2/96	187	unknown	
B1638	control	M	3	16/2/96	210	unknown	

Appendix 6 Kaplan-Meier survival curves for control (solid black lines) and food areas (solid gray line) for each litter. Broken lines are the upper and lower 90% confidence limits associated with each curve, as calculated by Greenwood's standard error (Pollock *et al.* 1989).

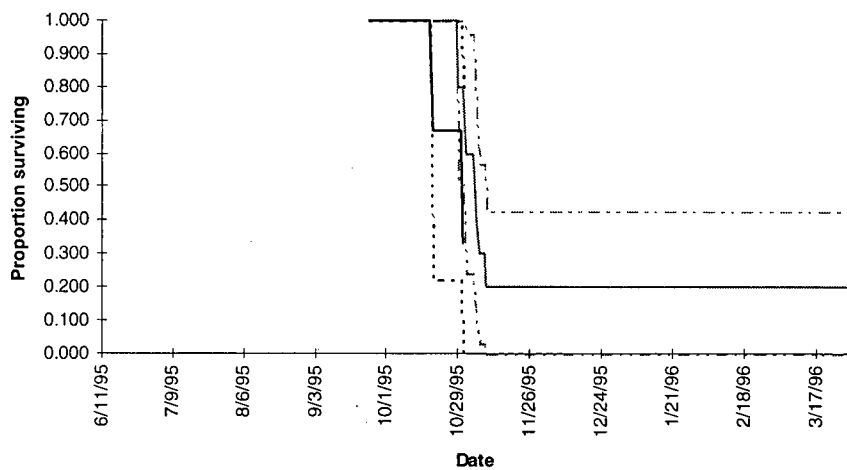


Appendix 6 Continued

Litter 3



Litter 4



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