

**REPRODUCTION, JUVENILE SURVIVAL AND MOVEMENTS OF  
SNOWSHOE HARES AT A CYCLIC POPULATION PEAK**

by

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## **ABSTRACT**

Snowshoe hare (*Lepus americanus*) populations were provided with supplemental food on two study grids in the southwest Yukon to examine the effects of food on reproduction and juvenile growth. Timing of parturition, pregnancy rates, litter sizes, male breeding condition, and juvenile growth rates were measured on the food grids and on two control grids during two summers at a cyclic peak in hare numbers. The main effects of food addition were to increase hare densities 2.1- to 2.7-fold, to advance the timing of breeding by about a week in one year, and to increase the mean size of third litter 30% in one year relative to the controls. There were no significant differences in pregnancy rates, litter sizes in five of six litter groups, length of male breeding season, or juvenile growth rates between hare populations on the food and control grids. Third litter stillborn rates were higher, and third litter juveniles grew slightly more slowly on food grids relative to those on controls, possibly because of higher densities. This study suggests that food is not a proximate factor limiting hare reproduction and early juvenile growth at the observed peak hare densities.

Juvenile snowshoe hares were radio-tagged at birth on one food addition grid and one control grid, to determine early juvenile survival rates, the effects of the food addition on these rates, and the proximate causes of mortality. Indices of survival were estimated by live-trapping on these grids, and on one additional set of grids. Thirty-day survival rates were 0.46, 0.15, and 0.43 for the first, second and third litters of the year, respectively. There

were no differences between early juvenile survival on the food addition and control grids in any of the litter groups. The main proximate cause of juvenile mortality was predation by small mammalian predators, the most important being red squirrels and arctic ground squirrels. Seventy percent of early juvenile mortality occurred during the first 5 days after birth. Survival of littermates was not independent; litters tended to all live or die as a unit more often than expected by chance. Fifty-one percent of litters had no known survivors after 14 days of age. Individual survival rates were negatively related to litter size, positively related to body size at birth, and litter size was negatively correlated with body size, suggesting trade-offs as predicted by life history theory. The number of recruits per litter, and the probability of total litter failure, did not differ significantly over the observed range of litter sizes.

The radio-tagged juveniles were also followed to examine pre-dispersal movements, maternal-juvenile interactions, and timing of natal dispersal. Hare litters stayed at their nest sites for an average of 2.7 days, after which each individual hare usually found a separate hiding place from its littermates. Juvenile hares ranged progressively farther from their nest sites as they grew, up to the age of 20 days. From 20 to 35 days of age, leverets stayed approximately 75 m from their nest sites, after which time their movements again increased. Observations at nest sites suggested that adult female hares nursed their litters only once per day, shortly after twilight. Some females aggressively defended their newborn litters before the juveniles left the nests. Natal dispersal of juvenile hares began shortly after

weaning at 24-28 days of age. Many third litter juveniles were nursed for a longer period of at least 29-40 days. Juvenile males may disperse sooner and travel farther than females from their natal ranges.

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## **GENERAL INTRODUCTION**

Cyclic fluctuations in abundance are characteristic of a number of species of mammals and birds. Most notable are those species whose populations undergo multi-annual cycles characterized by regular periodicity and amplitudes which may be over several orders of magnitude. These species have attracted a great deal of attention from population ecologists, since their widely fluctuating densities provide excellent opportunities for examining processes of population regulation and limitation (Keith 1974; Sinclair 1989). The best-studied population cycles of vertebrates have been the 3-4 year cycles of many microtine rodents and lemmings (Chitty 1960; Krebs & Myers 1974), the 4-7 year "quasi-cycle" of red grouse (*Lagopus lagopus scoticus*) in Britain (Watson 1967; Watson & Jenkins 1968; Potts, Tapper & Hudson 1984), and the "10-year" cycle of snowshoe hares (*Lepus americanus*) and their major predators in North America (Elton & Nicholson 1942; Keith & Windberg 1978). No generalities have emerged regarding a common cause or causes of population cycles. Models have been developed invoking many factors as the primary causes of the demographic changes related to population fluctuations, including changes in spacing behaviour, either genotypically (Chitty 1967; Krebs 1978) or phenotypically (Christian & Davis 1964) induced, food limitation (e.g. Keith & Windberg 1978), predation (e.g. Angelstam, Lindström & Widén 1984; Henttonen *et al.* 1987; Hanski, Hansson & Henttonen 1991), parasite-weather interactions (Potts, Tapper & Hudson 1984), and other multi-factor interactions (e.g. Lidicker 1985).

Snowshoe hare populations undergo cyclic fluctuations in abundance, with peaks occurring every 8-11 years (Elton & Nicholson 1942), in approximate synchrony throughout the boreal forest of North America (Smith 1983). Based on observations of two complete cycles in Alberta, L. B. Keith and colleagues (Keith 1974; Keith & Windberg 1978; Keith *et al.* 1984) developed a conceptual model of the principle interactions generating the snowshoe hare cycle. They considered the hare-vegetation interaction to be the driving force behind the cycle, and suggested that a shortage of winter browse at peak hare densities was the primary factor causing the population decline. These authors postulated that starvation was the largest cause of mortality at the beginning of the decline, but that predation became more important as the decline progressed (Keith *et al.* 1984). Their model was supported by the results of two experimental studies which monitored the demography of hare populations supplied with supplemental food, relative to control populations (Windberg & Keith 1976a; Vaughan & Keith 1981). Both of these studies found higher reproductive output, survival, and juvenile growth rates in the experimental populations.

Results of studies in the Yukon, however, showed that providing supplemental food to snowshoe hare populations failed to prevent the hares from declining in numbers (Krebs *et al.* 1986). While there was evidence of heavy browsing and relative food shortage at peak densities on the Yukon study grids (Sinclair *et al.* 1988; Smith *et al.* 1988), most mortalities were caused by predation (Boutin *et al.* 1986; Trostel *et al.* 1987). These authors concluded that food shortage was not a necessary cause of population

declines, and suggested that predation may be a necessary, and in some circumstances, the only cause of hare cycles (Krebs *et al.* 1986; Sinclair *et al.* 1988; Smith *et al.* 1988). Trostel *et al.* (1987) developed a simulation model which showed that predation at the levels observed in the Yukon could cause cycles of 8-11 years.

Little attention has been paid to the role of the spacing behaviour of snowshoe hares in population regulation. While models of intrinsic population regulation through spacing behaviour are a dominant paradigm for small mammals (Caughley & Krebs 1983; Krebs 1985), it is generally assumed that social behaviour plays no role in lagomorph population dynamics (Krebs 1986). However, experimental removal studies have indicated that resident hares may limit juvenile immigration and recruitment (Boutin 1984), and observations of penned hares have shown that they may aggressively react to strange conspecifics (Graf & Sinclair 1987). It is not known whether this spacing behaviour has any important demographic consequences.

While there is no consensus regarding the cause of the snowshoe hare cycle, the demographic changes associated with the decline have been more consistent between study areas. All three major investigations of the hare cycle have found that juvenile survival was the parameter most highly correlated with the rate of population change (Green & Evans 1940; Keith & Windberg 1978; Krebs *et al.* 1986). While Green & Evans (1940) reported that adult survival rates were constant over the cycle in Minnesota, both the Alberta (Keith & Windberg 1978) and the Yukon (Krebs *et al.* 1986) studies

found lower adult survival during the population declines. Reproductive rates may also vary with the cycle. Based on autopsies of shot animals, Cary & Keith (1979) reported that reproductive output varied 2.4-fold over the cycle, with peak reproduction occurring three years before the population peak. They attributed lower reproduction at peak and declining hare densities to food shortage. Reproductive output was not measured in the Yukon study (Krebs *et al.* 1986), but a recruitment index, which combined reproduction, early juvenile mortality and emigration, varied 5.3-fold over the cycle, and was significantly correlated with the rate of population change. Dispersal rates were highest at peak hare densities in both the Alberta and Yukon studies (Windberg & Keith 1976b; Boutin *et al.* 1985), but Boutin *et al.* (1985) concluded that losses of animals to dispersal were too low to cause the population decline.

One missing piece thus far in the studies of the demographic mechanisms causing population fluctuations of snowshoe hares has been the survival rates of juvenile hares before weaning (at about 28 days, Severaid 1942). Snowshoe hares do not make nests, and apparently only nurse their litters once per day for about 5-10 minutes (Severaid 1942; Rongstad & Tester 1971; Graf & Sinclair 1987). Hare litters are therefore very difficult to locate in the field. Juvenile hares do not enter live-traps until they are about 4 weeks old, and therefore early survival rates have not yet been measured. Based on an index of hare survival to 45 days of age (using the ratio of juveniles to adults in live-traps), Keith & Windberg (1978) concluded that changes in early juvenile survival were not important in causing population

fluctuations. Krebs *et al.* (1986), however, suggested that recruitment rate was strongly affected by early survival of juvenile hares. Their recruitment index, which was highly correlated with population trends, was primarily set by summer trapping results. Summer mortality of juveniles though, as measured by live-trapping juveniles older than 4 weeks, was not well correlated with the rate of population change, and the authors concluded that the important summer mortality must occur before the juveniles enter live-traps (Krebs *et al.* 1986).

The objectives of this study were two-fold: first, to experimentally examine the effects of food on snowshoe hare reproduction and early juvenile survival; secondly, to directly measure rates of early survival of juvenile hares, to determine the most important proximate causes of mortality, and to examine the movements and behaviour of young hares that might affect survival. The results of the study are presented in three parts. Chapter 1 reports on the effects of supplemental feeding on reproductive output and juvenile growth rates of wild hares. Chapter 2 examines the survival rates of juvenile hares to the age of weaning, summarizes the main causes of mortality, and examines life history characteristics that might affect survival. Finally, Chapter 3 presents data on juvenile movements before the age of weaning, and preliminary findings about the timing and distance of dispersal. This study represents the first attempt to fill in the missing pieces of snowshoe hare demography concerning early survival and ecology of young leverets.

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# **CHAPTER 1: EFFECTS OF SUPPLEMENTAL FOOD ON SNOWSHOE HARE REPRODUCTION AND GROWTH AT A CYCLIC POPULATION**

## **PEAK**

### ***INTRODUCTION***

There is little doubt that a finite food supply can act to limit the size and growth of animal populations. However, populations may be regulated, at densities well below those at which food shortages occur, by a number of other factors such as predation or spacing behaviour (Lack 1954; Watson & Moss 1970; Sinclair 1989). In an effort to clarify the role of food as a proximate factor limiting population size, many animal ecologists have experimentally augmented food supplies and observed the dynamics of the provisioned populations. Boutin (1990) recently reviewed the results of food addition experiments with terrestrial vertebrate populations, and noted that most studies have found that populations supplemented with food have 1) population densities two to three times higher, 2) higher mean body weights, and 3) advanced breeding relative to control populations. Therefore, many authors have concluded that food may indeed limit the density of natural populations.

While food addition can affect density and many demographic characteristics (e.g. pregnancy rates, litter sizes, survival rates) of animal populations, it generally has not altered patterns of population change (Boutin 1990). In particular, the addition of food has not prevented major population declines of many small mammal species that undergo periodic

cyclic fluctuations in numbers (e.g. Krebs & DeLong 1966; Cole & Batzli 1978; Ford & Pitelka 1984, Krebs *et al.* 1986).

Snowshoe hare (*Lepus americanus*) populations fluctuate widely in a "10-year" cycle, more or less synchronous throughout the North American boreal forest (Smith 1983), with peak numbers occurring every 8-11 years (Elton & Nicholson 1942). Keith (Keith 1974; Keith & Windberg 1978) hypothesized that hare populations decline from peak abundance due to winter food shortage, although predation on malnourished hares may be the main proximate cause of mortality (Keith *et al.* 1984). Support for the Keith hypothesis was provided from three short-term food addition studies with captive and insular hare populations (Windberg & Keith 1976; Pease, Vowles & Keith 1979; Vaughan & Keith 1981). These studies found that demographic parameters including reproductive rates, juvenile survival rates and body growth rates were adversely affected by food shortage, and significantly related to winter body weight loss. The same trends in these parameters were observed by Keith during three cyclic declines in Rochester, Alberta. In a field experiment with snowshoe hares in the Yukon, however, it was found that food addition did not prevent the cyclic population decline (Krebs *et al.* 1986). These authors concluded that, contrary to the Keith hypothesis, food shortage was not a necessary factor causing the decline, even though some animals may have been undernourished at peak densities (Krebs *et al.* 1986, Sinclair *et al.* 1988, Smith *et al.* 1988).

While overwinter juvenile mortality was the demographic parameter most closely associated with the rate of population change in Keith's studies

(Keith & Windberg 1978), major changes in reproductive output (i.e. pregnancy rates, ovulation rates, litter sizes and breeding season length) were also closely associated with the cycle in population density. Cary & Keith (1979) presented a detailed analysis of reproductive change in the hare cycle and concluded that most reproductive parameters cycled in synchrony, resulting in a 2.4-fold increase in potential natality from the low to the peak in the reproductive cycle. The peak in reproduction preceded the population density peak by about three years, and at maximum hare densities, reproductive output had already declined considerably. Cary & Keith (1979) attributed this to the effect of food shortage at peak densities. In the Yukon study, reproductive parameters were not directly measured, but an index of recruitment (number of juveniles trapped per adult female) was highly correlated with the rate of population change (Krebs *et al.* 1986).

This study was conducted in conjunction with a continuing experimental examination of the snowshoe hare cycle in the Yukon (Kluane Boreal Ecosystem Project). The objectives of my study were to determine the effects of food addition on 1) the reproductive parameters of the population and 2) the growth rates of juvenile hares. The hare populations in the Kluane region reached peak densities in 1989 and 1990, and began to decline over the winter 1990-91 (C. J. Krebs, unpublished data). The two years of this study, 1989 and 1990, thus coincided with high hare numbers. I used control and experimental grids established by the Kluane Project for this study.

## **METHODS**

The study area was located in the Kluane Lake region of southwest Yukon Territory, Canada (61°N, 138°W). The dominant vegetation of the area was white spruce forest (*Picea glauca*), with a dense but patchy shrub understory of mostly willow (*Salix glauca* and *S. alaxensis*), soapberry (*Shephardia canadensis*) and bog birch (*Betula glandulosa*) (Douglas 1974).

### **Hare Trapping**

I chose four 36-ha study grids each year for this study. Two of these were Kluane Project food addition grids--Agnes and Gravel Pit (referred to as Food1 and Food2 grids in this paper)--and two were controls. In 1989, I used the Kluane Project control grids Chitty and Sulphur (referred to as Control1 and Control2 in this paper), but in 1990 I switched one of my controls from Sulphur to Lloyd grid (referred to as Control2 in 1990) due to low sample sizes on Sulphur. On the food grids, commercial rabbit chow (16% crude protein) was distributed every 5-10 days, so that food was available *ad libitum* for the hares, along four cut lines spaced evenly across the grids. Food addition was commenced on the Food1 grid in 1986, and on Food2 in 1988. The food was placed in 16 evenly-spaced culvert feeders until the summer of 1989, when disturbance to the feeders by grizzly bears prompted a switch to free distribution of the food along the cut lines.

Eighty-six live Tomahawk traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin) were placed on each grid at stations 30 m apart. I trapped hares on all four grids for at least two days every other week from

May to September, 1989 and 1990. On several occasions disturbance of the traps by bears caused postponement of trapping sessions. Upon capture, each hare was weighed with a spring scale, its right hind foot was measured as an index of body size, and a monel ear tag (#3, National Band and Tag Co., Newport, Kentucky) was placed in its right ear. The reproductive condition of males was noted as scrotal, testes receding, or abdominal, based on testes size and position. I distinguished between pregnant and non-pregnant females only in the week before birth, when the increased body size of pregnant females was apparent. Females were also classified as lactating-nursing, lactating-not nursing, and not lactating.

### **Measurement of Litters**

Snowshoe hares do not have burrows or make nests (Severaid 1942; Graf & Sinclair 1987), and thus their litters are very difficult to locate in the field. In order to estimate litter sizes, I trapped pregnant females shortly before parturition, and placed them in 60 X 60 X 120 cm chicken wire cages covered with burlap and provided with ample spruce branches and grass for natural cover. I attempted to capture 10-15 females per grid for each litter group. On control grids, the cages were placed within each female's home range, adjacent to her capture site. However, due to disturbance of cages by bears on the food grids, all cages were placed within small (0.05-1.0 ha) enclosures surrounded by electric fences. I transported pregnant females to and from these "nurseries" upon capture and after parturition. Female hares spent a mean of 6.2 days in these cages before giving birth to their litters.

Upon parturition, female hares were immediately released. On the control grids, females were simply let out of their cages. On the food grids, they were carried with their litters back to their home ranges where "nests" were made for the newborn hares. The females were left next to the nests in covered open traps, which they could leave when they were ready. I counted each hare litter, and weighed, measured (right hind foot length), sexed, and ear-tagged (#1 monel tags) the individual leverets before they were released. On two of the grids (Food1, Control1), I also affixed 2-g radio transmitters (Models SR-1 and SR-2, Biotrack, Dorset, England) with glue to the backs of half of the juveniles in each litter to look at subsequent survival (Chapter 2). I attempted to recapture all radioed leverets after approximately ten days to measure growth rates and re-glue radios.

### **Determination of Reproductive Parameters**

As male snowshoe hares become scrotal during the late winter (Cary & Keith 1979, Boutin 1984a), I was unable to determine the timing of onset of breeding condition in males because I started trapping each year in May. I did, however, record the chronology of testes regression in late summer from trapping data. The mean dates of parturition of caged hares were calculated as measures of the timing of breeding on each of the study grids. Over the course of the study, seven out of 201 pregnant females died in cages or traps, and I autopsied these to gain additional data on litter sizes and timing of parturition. I determined the age of hare embryos based on published

chronologies of snowshoe hare prenatal development (Bookhout 1964; Dell & Schierbaum 1974).

Snowshoe hares are a multi-littered species with post-partum oestrus and synchronous breeding (Severaid 1942). Juveniles are thus born in distinct litter groups during the summer, spaced apart by about 35-40 days (Severaid 1942). I calculated pregnancy rates and litter sizes for each litter group separately.

Pregnancy rates per litter group were estimated from the proportion of trapped females obviously pregnant, or having just given birth during a period of one week either side of the mean parturition date for the grid. I used litter sizes from caged and autopsied females as measures of mean natality per litter group.

### **Statistical Procedures**

I estimated the population sizes on each grid from the summer trapping data using the Jolly-Seber model (Seber 1982). These estimates are probably biased to an unknown degree, because hares violate the assumption of equal catchability (Krebs *et al.* 1986), but they are useful indices of relative population sizes among the grids.

I calculated indices of spring condition for adult males from May trapping data, using the relationship between body weight and right hind foot length, as in Bailey (1968). A power curve was fitted to the weight and foot length measurements (using the NONLIN module, SYSTAT, Inc., Evanston, Illinois) from all Kluane Project May trapping data for males on

the control grids in 1989 and 1990. The resulting relationship,  $WT(g) = 738.9 + RHF(mm)^{1.3}$ , was used to calculate a predicted weight for a hare with a given right hind foot length. The condition index for that hare was then calculated as observed weight/predicted weight. Condition indices were calculated for males only, as most females were pregnant when May trapping commenced, and their weights were influenced by their gestation stage.

Gompertz growth curves were fitted to the observed body weights of trapped and radioed juvenile hares (sexes combined) according to the methods of Kaufmann (1981). In preliminary analyses, Gompertz growth curves fit the hare growth data better than logistic or Bertalanffy curves. Growth rates were thus measured as "specific growth rates", or the percent increase in size per day. I compared growth rates by testing for significant differences between the slopes of the regression lines of the differentiated growth equations plotted on a semi-logarithmic scale (Kaufmann 1981).

All ANOVAs, t-tests, linear regressions, and G-tests were performed according to procedures in Zar (1984).

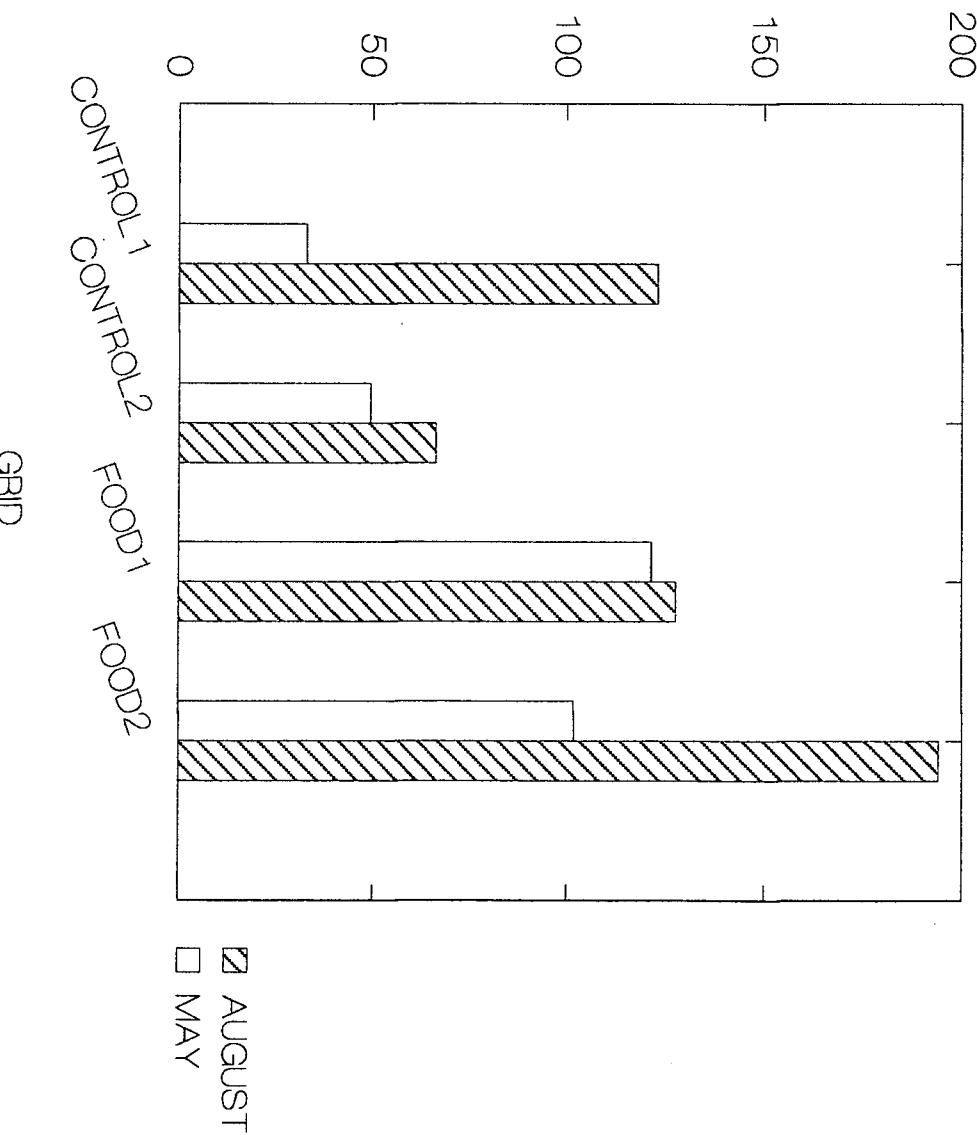
## **RESULTS**

### **Population Density**

Hare population sizes in spring on the food grids were much higher than those on the controls in both years (Figure 1.1, 1989 - 2.7 X higher; Figure 1.2, 1990 - 2.1 X higher). Population estimates were highly variable on the food grids during the two summers, and on Control2 grid in 1990.

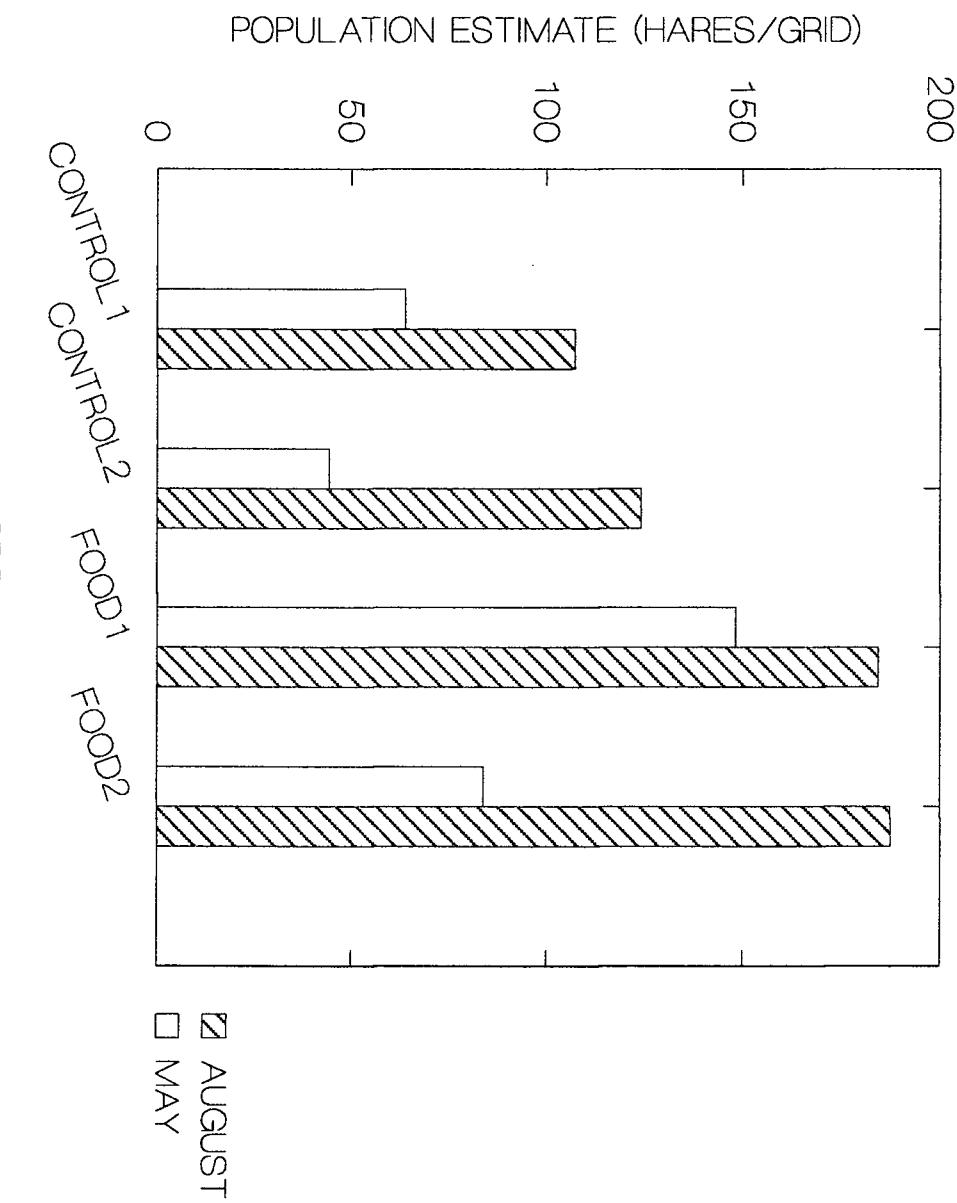
**Figure 1.1.** Jolly-Seber population estimates of snowshoe hares on four study grids in summer 1989.

POPULATION ESTIMATE (HARES/GRID)



**Figure 1.2.** Jolly-Seber population estimates of snowshoe hares on four study grids in summer 1990.

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This may have been partly due to high movement rates on and off the food grids relative to feeding schedules. The population on Control 1 grid steadily increased through the summer in both years. There were no general trends of population increase or decrease between the two years of study.

### **Spring Body Weights and Condition Indices**

Body weights and condition indices of adult male hares in spring indicated the same differences between animals on the food and control grids (Tables 1.1 and 1.2). Males on the food grids were about 10% heavier and in better body condition in May than those on controls in 1990 (Nested ANOVA, body weights,  $0.025 < P < 0.05$ ; condition indices,  $0.025 < P < 0.05$ ), but not in May 1989.

### **Timing of Testicular Regression**

Testicular regression was first apparent in the second half of July on both food and control grids (Food - 73.3% scrotal; Control - 60.4% scrotal), by mid-August fewer than half of the males were fully scrotal (Food - 31.6%; Control - 35.3%), and by late August all males were abdominal or had receding testes. Therefore, food addition had no apparent effect on the cessation of breeding in males.

### **Pregnancy Rates**

Most female hares on the study grids had three litters during the summers of 1989 and 1990 (Table 1.3). The pregnancy rate was nearly 100%

Table 1.1: Body weights ( $\pm$  S.D.) of male snowshoe hares in spring on study grids (sample sizes in parentheses).

Year	Body Weights (g)			
	Food1	Food2	Control1	Control2
1989	$1364 \pm 136$ (43)	$1321 \pm 106$ (12)	$1286 \pm 137$ (16)	$1326 \pm 119$ (27)
1990*	$1441 \pm 124$ (53)	$1411 \pm 174$ (23)	$1270 \pm 134$ (34)	$1332 \pm 124$ (14)

\* Significant difference between food and control grids,  $P < 0.05$ .

Table 1.2. Condition indices<sup>a</sup> ( $\pm$  S.D.) of male snowshoe hares in spring on study grids (sample sizes in parentheses).

Year	Condition Indices			
	Food1	Food2	Control1	Control2
1989	1.034 $\pm$ 0.098 (43)	1.014 $\pm$ 0.082 (12)	0.992 $\pm$ 0.098 (16)	1.007 $\pm$ 0.082 (27)
1990*	1.098 $\pm$ 0.091 (53)	1.075 $\pm$ 0.135 (22)	0.977 $\pm$ 0.100 (34)	1.017 $\pm$ 0.087 (14)

\* Significant difference between food and control grids,  $P < 0.05$ .

a Observed weight/predicted weight; predicted weight calculated from power curve fitted to weight and right hind foot length data for all male hares captured on control grids during May in 1989 and 1990,  $WT(g) = 738.9 + RHF(mm)1.3$ .

Table 1.3. Pregnancy rates of adult female hares on study grids (sample sizes in parentheses).

		Pregnancy Rates (%)			
Year	Litter	Food1	Food2	Control1	Control2
1989	1	92.9 (42)	90.3 (31)	100.0 (11)	90.5 (21)
	2	100.0 (21)	100.0 (46)	94.1 (17)	100.0 (14)
	3	95.5 (22)	97.2 (36)	82.4 (17)	82.4 (17)
1990	1	100.0 (80)	97.4 (39)	91.7 (36)	87.1 (31)
	2	96.8 (31)	97.2 (36)	96.6 (29)	95.7 (23)
	3	73.1 (26)	94.1 (51)	81.5 (27)	91.3 (23)

on all grids for the first two litters of the year. In 1989, the third litter pregnancy rate was slightly lower (82.4% vs 96.6%) on the control grids, but in 1990, pregnancy rates of control and food grids were similar (83.6% and 86.4%, respectively).

### **Timing of Litters**

The mean date of parturition was advanced by approximately one week in 1989 on the food grids relative to the controls (Table 1.4, Litter 2, Nested ANOVA,  $0.025 < P < 0.05$ ; Litter 3, Nested ANOVA,  $P < 0.0005$ ). Although litters were generally earlier on the food grids in 1990 as well, these differences were smaller (3-4 days) and not statistically significant. Females on the control grids gave birth to litters significantly earlier in 1990 than in 1989 (ANOVA,  $0.025 < P < 0.05$ ).

### **Evidence of Superfoetation**

The European hare (*Lepus europaeus*) is able to shorten the interval between successive litters by successfully mating during a pre-partum oestrus several days before the birth of a litter in gestation (Martinet, Legouis & Moret 1970). In this way, the female can be pregnant with two litters, each at different stages of development, at the same time ("superfoetation"). Flux (1981) suggested that this may occur in snowshoe hares as well. The gestation period of snowshoe hares is 36-37 days (Severaid 1942).

Table 1.4. Mean parturition dates ( $\pm$  S.D.) of hare litters born in cages on study grids (sample sizes in parentheses).

Year	Litter	Mean Parturition Date			
		Food1	Food2	Control1	Control2
1989	1	21 May $\pm$ 1.7d (8)	---	25 May $\pm$ 1.9d (8)	---
	2*	22 Jun $\pm$ 2.4d (9)	25 Jun $\pm$ 1.8d (8)	2 Jul $\pm$ 3.5d (8)	4 Jul $\pm$ 2.9d (5)
	3***	1 Aug $\pm$ 3.5d (9)	31 Jul $\pm$ 2.0d (7)	7 Aug $\pm$ 4.1d (5)	8 Aug $\pm$ 2.1d (2)
1990	1a	19 May $\pm$ 2.5d (15)	22 May $\pm$ 1.5d (11)	26 May $\pm$ 1.4d (7)	24 May $\pm$ 2.8d (7)
	2	23 Jun $\pm$ 2.2d (11)	26 Jun $\pm$ 4.7d (16)	28 Jun $\pm$ 3.5d (14)	26 Jun $\pm$ 4.0d (13)
	3	29 Jul $\pm$ 2.4d (9)	25 Jul $\pm$ 2.8d (11)	1 Aug $\pm$ 1.9d (12)	30 Jul $\pm$ 1.4d (7)

\* Significant difference between food and control grids,  $P < 0.05$ .

\*\*\* Very highly significant difference between food and control grids,  $P < 0.001$ .

a No statistical tests made, as many females on control grids gave birth to first litter before trapping was conducted on grids.

In my study, the intervals between litter groups, based on mean parturition dates, varied from 27.5 to 39.5 days on the study grids. The mean interval was 37.4 days for the 37 individual females for which the date of birth was known. I found evidence suggesting intervals between litters of less than 35 days in only two cases. When trapped in July 1989, two females on the Control 1 grid appeared to have recently given birth to third litters, less than 30 days after their second litters dropped. However, I could not find the nests of these two females to confirm that they did exhibit superfoetation. If it does occur, superfoetation does not appear to be common in snowshoe hares at Kluane. No evidence of superfoetation has been observed in a colony of captive snowshoe hares held at the University of British Columbia either (A. R. E. Sinclair, personal communication).

### **Litter Sizes**

Mean litter sizes were significantly larger on the food grids only for the third litter group in 1990 (Table 1.5, Nested ANOVA,  $0.025 < P < 0.05$ ). An increase in third litter size on the food grids from 1989 to 1990 was the main reason for this difference. Generally, first litters tended to be the smallest and second litters the largest of the summer.

### **Stillborn Rates**

A surprisingly large number of newly-born hares were stillborn in the cages (Table 1.6), although almost all were fully formed and of the same weights as live littermates. I found no evidence of female hares eating their

Table 1.5. Mean litter sizes ( $\pm$  S.D.) of hare litters born in cages on study grids (sample sizes in parentheses).

		Mean Litter Sizes			
Year	Litter	Food1	Food2	Control1	Control2
1989	1	$3.8 \pm 1.2$ (9)	---	$3.6 \pm 0.7$ (8)	---
	2	$5.6 \pm 1.7$ (9)	$7.1 \pm 1.5$ (9)	$5.9 \pm 1.6$ (8)	$6.2 \pm 0.8$ (5)
	3	$4.6 \pm 1.1$ (9)	$5.1 \pm 2.0$ (7)	$4.2 \pm 0.4$ (5)	$5.5 \pm 0.7$ (2)
1990	1	$3.8 \pm 0.7$ (15)	$3.5 \pm 0.8$ (11)	$3.9 \pm 0.9$ (7)	$4.0 \pm 0.8$ (7)
	2	$5.5 \pm 2.2$ (11)	$6.6 \pm 0.8$ (16)	$5.7 \pm 1.4$ (14)	$5.8 \pm 1.2$ (13)
	3*	$5.8 \pm 1.2$ (10)	$5.5 \pm 1.1$ (13)	$4.1 \pm 1.6$ (12)	$4.6 \pm 1.3$ (7)

\* Significant difference between food and control grids,  $P < 0.05$ .

Table 1.6. Stillborn rates (% of total young born dead) for hare litters born in cages on study grids (sample sizes in parentheses).

Year	Litter	Stillborn Rates (%)			
		Food1	Food2	Control1	Control2
1989	1	3.6 (28)	---	0.0 (29)	---
	2	6.0 (50)	6.3 (64)	0.0 (47)	19.4 (31)
	3	43.9 (41)	45.2 (31)	4.8 (21)	9.1 (11)
1990	1	9.5 (52)	17.6 (34)	14.8 (27)	0.0 (28)
	2	1.6 (61)	17.6 (74)	2.5 (80)	9.2 (76)
	3	18.9 (53)	29.1 (66)	8.2 (49)	21.9 (32)

stillborn young, so I believe I was able to count them accurately. Stillborn rates were fairly low (0-18%) in the first and second litter groups, but were higher in third litters, especially on the food grids where stillborn rates approached 50% in 1989. Necropsies of the stillborn young revealed no obvious pathology, nor were any pathogenic viruses or bacteria found in lab cultures of lung, liver, and small intestine tissues. Trace mineral levels were also similar between stillborn and predator-killed young.

### **Total Reproductive Output**

An estimate of total reproductive output per female surviving the breeding season was made by multiplying pregnancy rates by mean litter sizes and (1 - stillborn rates), and summing these over the three litter groups (Table 1.7). This corresponds to Keith's "potential natality" (Cary & Keith 1979). There were no significant differences between the food and control grids in either year.

### **Sex Ratios**

Sex ratios of newly-born leverets differed statistically from 1:1 in only one case out of 22 total litter groups on the four study grids (Table 1.8), a rate not different from that expected by chance at  $P = 0.05$ . These results therefore suggest that the sex ratio of hares born at peak numbers was even.

### **Body Weights of Newborn Hares**

There were no significant differences between the mean body weights

Table 1.7. Total estimated reproductive output<sup>a</sup> per surviving female on study grids.

Year	Reproductive Output (Juveniles/Female)			
	Food1	Food2	Control1	Control2
1989	11.1	14.1 <sup>b</sup>	12.5	12.4 <sup>b</sup>
1990	12.1	11.8	11.5	11.8

<sup>a</sup> Total reproductive output = (pregnancy rate)(mean litter size)(1 - stillborn rate), summed over three litter groups.

<sup>b</sup> Mean first litter size estimated from other food grid or control grid.

Table 1.8. Sex ratios of hare litters born in cages on study grids (proportion of females, number of juveniles in parentheses).

Year	Litter	Sex Ratios			
		Food1	Food2	Control1	Control2
1989	1	0.50 (20)	---	0.43 (21)	---
	2	0.59 (29)	0.57 (47)	0.60 (47)	0.48 (31)
	3	0.67 (33)	0.60 (10)	0.55 (20)	0.45 (11)
1990	1	0.58 (52)	0.67 (33)	0.52 (23)	0.54 (24)
	2	0.43 (61)	0.47 (72)	0.51 (80)	0.63 (73)*
	3	0.40 (52)	0.54 (61)	0.41 (49)	0.50 (32)

\* Significantly different from 1:1, P < 0.05.

of newly-born hares on food grids and those on controls in any single litter group, nor were there any significant differences in total litter biomasses between treatments (Table 1.9). If all juvenile weights from the two years are analysed together in an ANOVA with two levels of nesting (adult females within grids, grids within treatments), the effect of food is significant ( $P = 0.007$ ), with juveniles on food grids being significantly lighter than those on control grids. However, the difference between the mean weights is slight (59.7 g vs 61.0 g), and it is doubtful that this is biologically meaningful. In general, body size of third litter juveniles was the largest, especially on the control grids. Mean body weight of the litters was significantly negatively correlated with litter size ( $r = -0.49$ ,  $P < 0.001$ ), a result not found by Severaid (1942), but noted for hares in general by Flux (1981).

### **Growth Rates of Juvenile Hares**

The growth rates of juvenile hares (sexes combined) were not significantly different between the food and control grids for any of the three litter groups (Figures 1.3, 1.4, and 1.5). The Gompertz growth curves for the first two litter groups were nearly identical for the experimental and control grids, although the food grids have higher asymptotic values. From birth to age 60 days, first litter leverets gained an average of 16.3 g and 16.0 g, and second litter juveniles 14.6 g and 14.1 g per day on the food and control grids, respectively. Growth was nearly linear for the first 2-3 months. There was a trend for growth to be slower on food grids for the third litter group (Figure 1.5), but data were lacking for third litter juveniles older than 35 days. The

Table 1.9. Mean juvenile weights at birth ( $\pm$  S.D.) for hare litters born in cages on study grids (number of litters in parentheses).

Mean Juvenile Weights (g)					
Year	Litter	Food1	Food2	Control1	Control2
1989	1	60.7 $\pm$ 8.8 (6)	—	53.6 $\pm$ 7.1 (8)	—
	2	60.0 $\pm$ 8.3 (9)	53.4 $\pm$ 13.1 (8)	54.4 $\pm$ 14.0 (8)	54.2 $\pm$ 5.3 (4)
	3	63.4 $\pm$ 7.5 (8)	65.0 $\pm$ 13.8 (4)	73.0 $\pm$ 12.7 (5)	60.0 $\pm$ 4.8 (2)
1990	1	68.1 $\pm$ 8.8 (13)	63.4 $\pm$ 7.8 (10)	57.7 $\pm$ 15.2 (6)	62.6 $\pm$ 6.4 (6)
	2	63.2 $\pm$ 7.7 (11)	54.3 $\pm$ 8.6 (9)	60.8 $\pm$ 11.7 (14)	58.1 $\pm$ 8.7 (12)
	3	67.6 $\pm$ 5.3 (9)	52.3 $\pm$ 9.5 (10)	79.4 $\pm$ 13.9 (11)	74.3 $\pm$ 8.3 (6)

Figure 1.3. Gompertz growth curves of first litter juvenile snowshoe hares (mean birth dates 19-26 May) on food and control grids in 1989 and 1990 (sexes combined, only animals of known age plotted).

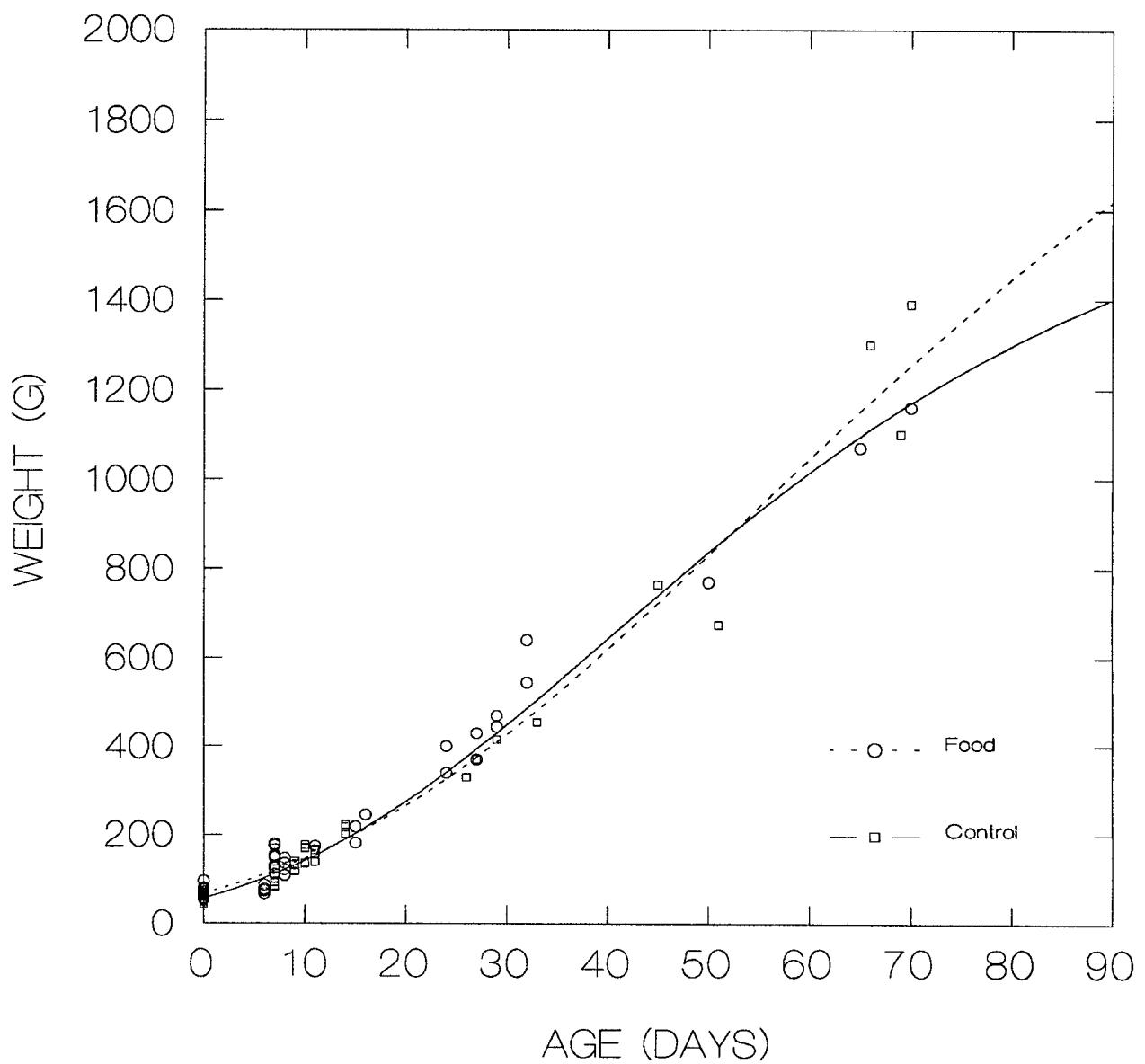
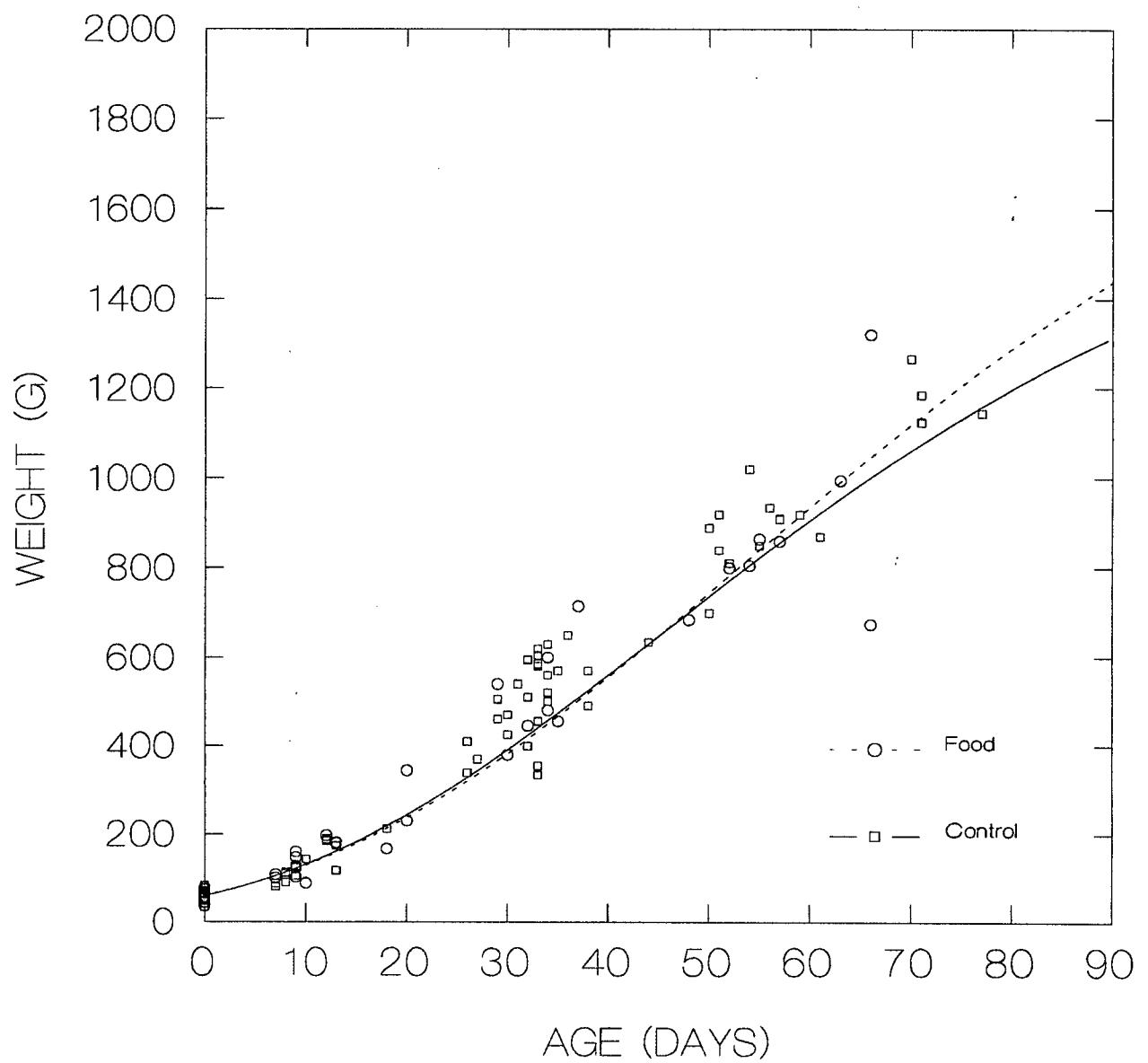
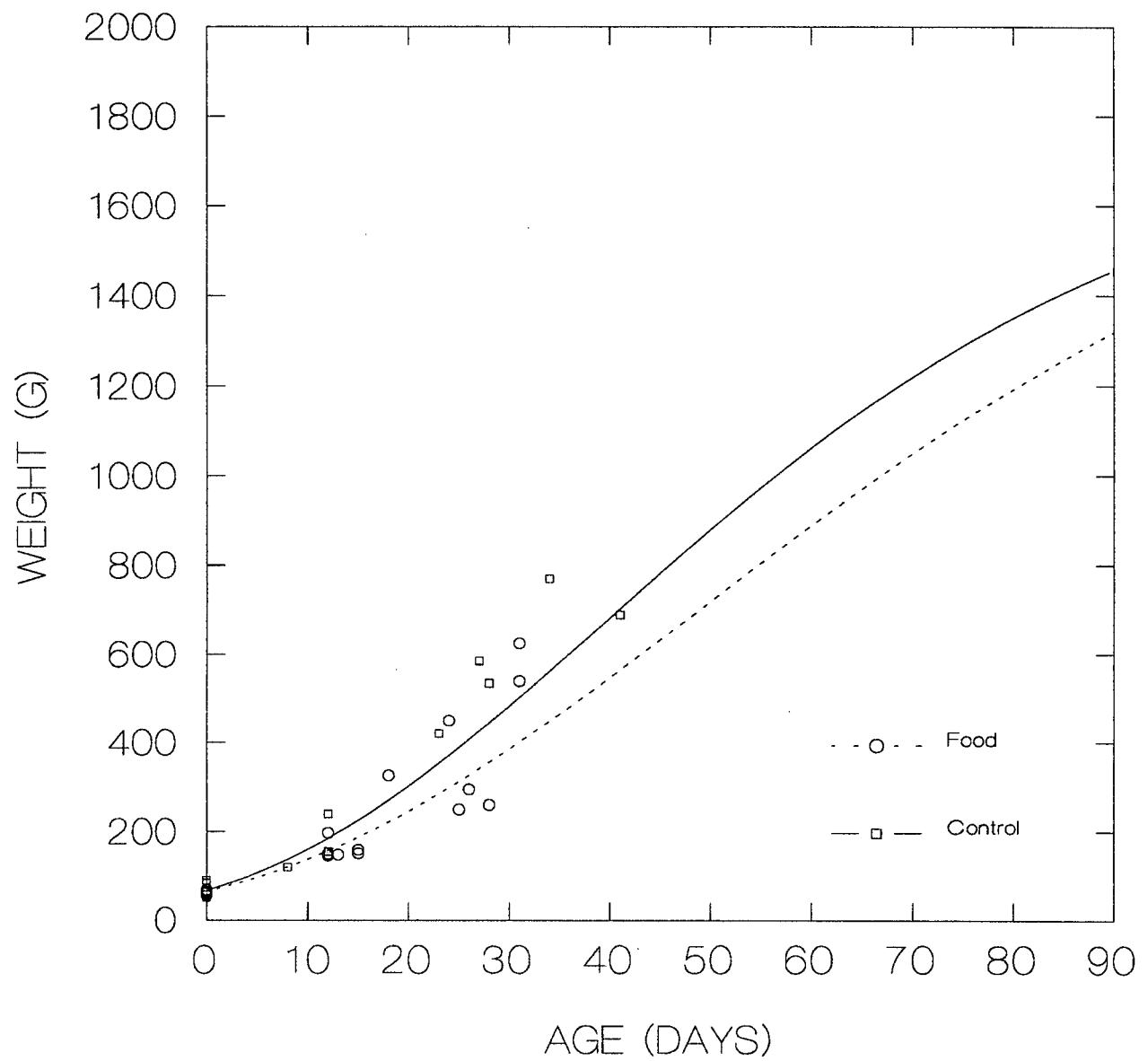


Figure 1.4. Gompertz growth curves of second litter juvenile snowshoe hares (mean birth dates 22 June-4 July) on food and control grids in 1989 and 1990 (sexes combined, only animals of known age plotted).



**Figure 1.5.** Gompertz growth curves of third litter juvenile snowshoe hares (mean birth dates 25 July-8 August) on food and control grids in 1989 and 1990 (sexes combined, only animals of known age plotted).



estimated growth rates to 60 days age on the food and control grids were 13.7 g and 16.6 g per day, respectively.

### **Juvenile Breeding**

Only one scrotal first litter juvenile was trapped during this study (a 1075 g juvenile male on Food1 grid, on 25 July 1989), and no juvenile females showed evidence of breeding. Keith & Meslow (1967) also noted that juvenile breeding is a rare event.

### ***DISCUSSION***

These results are consistent with the findings of many vertebrate food addition experiments in several respects. First, population sizes of hares on the food grids were 2-3 times those on the controls, as found in most such studies (Boutin 1990). The food addition therefore increased survival rates (as found by Boutin 1984a; Krebs *et al.* 1986), immigration rates (Boutin 1984a), or both on the food grids relative to the controls. I did not measure over-winter survival or recruitment rates, and so I do not know which demographic factor contributed the most to higher densities on the food grids. Second, body weights of the supplemented adult animals were also generally higher, at least in 1990. Third, the timing of female reproduction was advanced on the food grids in 1989, as reported in many other studies (e.g. Hansen & Batzli 1979 with *Peromyscus leucopus*; Vaughan & Keith 1981 with snowshoe hares; Taitt & Krebs 1983 with *Microtus townsendii*). The "onset of spring" was earlier in 1990 than in 1989 (i.e. higher temperatures

and earlier snow-melt), and this may have been the reason that female hares on the control grids were able to advance reproduction in 1990 to match the dates on food grids (Conaway & Wight 1962; Cary & Keith 1979). I did not measure the timing of testicular recrudescence in the winter, but there is evidence that males became scrotal 1-3 weeks earlier on the food grids at Kluane (Boutin 1984a; D. S. Hik, personal communication). Finally, the larger third litter sizes on the food grids in 1990 suggests that food did have some effect on hare reproduction.

However, the most striking pattern in these results is that the food addition had little or no effect on most of the demographic parameters measured. The timing of male testes regression was not different between treatments, contrary to the experimental results of Windberg & Keith (1976). Pregnancy rates were very high on all grids, and thus not markedly greater on the food grids, in contrast to what has been found in many studies of food-supplemented small mammal populations (e.g. Vaughan & Keith 1981; Ford & Pitelka 1984 with *Microtus californicus*; Bomford & Redhead 1987 with *Mus musculus*). Litter sizes were increased by the food addition in only one of six litter groups, as opposed to a clearer response in other studies (e.g. Kirkpatrick & Kibbe 1971 with *Sylvilagus floridanus*; Cole & Batzli 1978 with *Microtus ochrogaster*; Vaughan & Keith 1981; Dobson & Kjelgaard 1985 with *Spermophilus columbianus*). Juvenile growth was essentially the same on the food and control grids, with a possible trend towards lower growth of third litter juveniles on food addition grids. In previous studies, growth increased with food addition (e.g. Cole & Batzli 1978; Vaughan & Keith 1981;

Desy & Thompson 1983 with *Microtus pennsylvanicus*; Sullivan, Sullivan & Krebs 1983 with *Eutamias townsendii*). Most importantly, the overall reproductive output per female in my study was not greater in either year on the food grids.

Why did snowshoe hares not respond to the food addition with increased reproduction or juvenile growth rates? I consider three possibilities:

1) *Food was a proximate factor limiting reproduction and growth on the controls, but the food addition was inadequate to produce any response on the food grids.* The fact that the mean body weights and condition indices of adult males were greater on the food grids than on the controls suggests that some individuals did respond physiologically to food addition. Also, the advanced timing of parturition in 1989 and the larger third litter sizes in 1990 on the food grids are indicative that food did have some effect on hare reproduction. This possibility therefore seems unlikely.

2) *Food was a proximate factor limiting reproduction and growth on the controls, but while the food addition was adequate, density-related factors other than food were limiting on the food grids.* Hare densities were 2-3 times higher on the food grids than on the controls. These higher densities likely reflected the increased quality of the food grid habitat to hares due to the food addition. According to habitat selection theory, animals should distribute themselves among habitats relative to their expected fitness in each habitat (Fretwell & Lucas 1970; Rosenzweig 1981). Thus the most suitable habitats also have the highest animal densities. Fretwell & Lucas

(1970) hypothesized that "ideally" distributed animals will have the same mean expected fitness in all habitats, because the higher animal density in the best habitat decreases that habitat's suitability to the point where it is profitable (i.e. expected fitness would not be less) for animals to occupy more marginal habitat. Although reproductive output is only one component of inclusive fitness (see Morris 1989), I may have observed no differences in reproduction between the food and control grids due to adverse effects of factors related to the high density of hares on the food grids.

The main effect of density on reproduction in mammals is generally considered to operate through food limitation--at higher densities there is less food and greater nutritional stress on individual animals. In this experiment, food was presumably not limiting on the food addition grids. However, density may also affect a number of other factors in the animals' environment, for example by increasing the intensity of social interactions and the probability of parasite and disease transmission. These stresses may have acted to lower reproductive output on the food grids despite the food addition acting to increase it.

The effects of increased density on population dynamics of hares are little understood (Krebs 1986). There have been a number of hypotheses suggesting that behavioural changes in small mammals at high densities may cause population declines (Chitty 1960; Christian & Davis 1964). It is known that snowshoe hares form dominance hierarchies, and hares react aggressively towards subordinate conspecifics (Boutin 1984b; Graf 1985; Sinclair 1986). Whether or not increased stress due to social factors at high

densities could affect the demography of hares is unknown. The high stillborn rates in the third litter on the food grids suggest that females on these grids were more physiologically stressed than those on the controls. The cause of these stillbirths is unknown, but the high physiological costs of nursing two previous litters (Hanwell & Peaker 1977; Kenagy 1987) could have combined with higher socially-induced stress to contribute to the high rates of loss.

Higher hare densities could also lead to higher transmission rates of parasites, but preliminary analyses of fecal samples suggest that hares on food grids have lower parasite loads (A. R. E. Sinclair, unpublished data).

*3) Neither food nor density-related factors limited reproduction and juvenile growth at peak hare densities on the controls and food grids, so no response to food addition was observed.* Cary & Keith (1979) noted that peak hare reproduction occurred three years before the population peak, and was considerably lower at the highest hare density. They found correlations of most reproductive parameters with overwinter adult weight loss, and attributed the decline in reproduction to food shortage. This study found no important responses of hare reproduction and juvenile growth to food addition. The litter sizes and pregnancy rates that I observed on the control grids were higher than those recorded by Cary & Keith (1979) at peak densities in Alberta (although there is a general trend of increasing litter sizes from south to north in snowshoe hares; Keith, Rongstad & Meslow 1966). Likewise, the juvenile growth rates at Kluane (13.7-16.6 g/day) compared favorably to those recorded in the literature for captive hares with

unlimited food (+14.5 g/day, Keith, Meslow & Rongstad 1968; +17.1 g/day, Graf & Sinclair 1987), and are higher than those presented by Vaughan & Keith (1981) for food-stressed leverets (+9.8 g/day). These observations suggest that although food may have been limiting to reproduction and juvenile growth in Keith's Alberta study area, it was not in the Yukon in 1989 and 1990 at the observed peak hare densities. It remains possible that food will adversely affect reproduction and growth during the population decline at Kluane.

I cannot distinguish between the second and third above interpretations based on my experimental results. An experiment designed to separate the effects of density and food on hare demography is necessary to examine the relative effects of these factors. In the only experimental study examining the effects of density on hare demography, Vaughan & Keith (1981) concluded that density *per se* had little effect on hare reproduction, growth or survival. However, their "low density" treatment was 4.2 hares/ha, or about 1.5 times the mean fall density of hares observed at peak numbers on the food grids, and 2.4 times that observed on the controls (density was calculated for our Yukon data by adding a boundary strip of 90 m around the grids to correct for edge effect; see Bondrup-Nielsen 1983; Boutin 1984c). Their "high density" treatment was 13.2 hares/ha, or about 4.6 times the mean fall densities observed on the food grids. A factorial experiment designed to look at the relative effects of food and density-related factors at the lower densities observed at Kluane would better indicate their influence on hare demography. Direct measures of rates of social interaction (e.g. by

direct observation), indices of stress (e.g. physiological responses to artificially induced stress), parasite loads and demographic parameters could be made on captive hare populations stocked at different densities and supplied with food at different levels.

The results of this study suggest that food is not a proximate factor limiting hare reproduction or early juvenile growth at the observed peak densities in the Yukon. It is unknown whether the lower peak densities measured in the Yukon relative to those seen in Keith's study in Alberta could account for our conflicting results. If cyclic amplitude can affect the relative contributions of food and density-related factors to the hare decline, then it is important to conduct experiments at different peak densities to formulate a general model of the hare cycle.

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## **CHAPTER 2: EARLY SURVIVAL OF JUVENILE SNOWSHOE HARES**

### ***INTRODUCTION***

Snowshoe hare (*Lepus americanus*) populations undergo cyclic fluctuations in abundance throughout the North American boreal forest, with peak numbers occurring each 8-11 years (Elton & Nicholson 1942). L. B. Keith and colleagues have hypothesized that the dramatic population "crashes" that follow the peak years are caused by hare overbrowsing and subsequent food shortage (Keith & Windberg 1978; Keith *et al.* 1984). In this model, starvation of hares is the most important mortality factor at the beginning of the population decline, but predation becomes the predominant proximate cause of mortality as the decline progresses. However, studies in the Yukon showed that hare populations declined even when artificially supplemented with food (Krebs *et al.* 1986; Smith *et al.* 1988; Sinclair *et al.* 1988), indicating that food shortage is not a necessary factor in the population declines. Keith (1990) emphasized the importance of food shortage on a regional scale to hare demography, and suggested that local food additions were inadequate for testing the hare-food interaction model.

Snowshoe hare population declines are characterized by high mortality rates, particularly of juvenile hares (Green & Evans 1940; Keith & Windberg 1978; Keith *et al.* 1984; Krebs *et al.* 1986). Juvenile survival in the autumn and early winter was highly correlated with the rate of population change in studies of the hare cycle in Alberta and the Yukon (Keith & Windberg 1978; Keith *et al.* 1984; Krebs *et al.* 1986). The influence of early juvenile survival

in the summer on the rate of population change is less clear. Snowshoe hare litters are very difficult to locate in the field, and leverets do not enter live-traps before they are 3-4 weeks old. Therefore, no direct measures of snowshoe hare survival before weaning (at 28 days; Severaid 1942) have been made. Cary & Keith (1979) autopsied shot hares and found that reproductive rates varied 2.4-fold over the cycle in Alberta. Keith & Windberg (1978) used these rates and the ratio of live-trapped juveniles to adults to calculate indices of early juvenile survival. From these indices, they concluded that changes in the rates of juvenile hare survival before the age of 45 days did not significantly affect the pattern of population change. However, Krebs *et al.* (1986) suggested that early juvenile hare survival strongly affected recruitment rate in the Yukon. These authors did not directly measure reproductive output, but calculated a recruitment index based on the number of trapped juvenile hares per adult female in the population. This index varied 5.3-fold from the population increase to the decline, and was highly statistically correlated with the rate of population change. As summer survival of juveniles older than 4 weeks was poorly correlated with population trends, Krebs *et al.* (1986) concluded that the important summer mortality must have occurred before the juvenile hares reached trappable age.

This study was undertaken to determine the rates of early survival of juvenile hares, and was carried out in conjunction with a study of the effects of food addition on hare reproduction (Chapter 1). My objectives were to 1) directly measure survival rates of juvenile hares to weaning, 2) determine the

main proximate causes of mortality of juvenile hares, 3) determine the effects of food addition on juvenile survival, and 4) investigate whether there are trade-offs between litter size, juvenile body weight, and juvenile survival, as predicted by life history theory (Stearns 1976; 1977; 1989).

## **METHODS**

The study area and the general methods were the same as those described in Chapter 1.

On two of the grids (Food1 and Control1), I affixed 2-g radio transmitters (Models SR-1 and SR-2, Biotrack, Dorset, England) with glue to short-clipped fur between the shoulder blades of half of the juveniles in each litter. The radios had battery lives of about 6 weeks, and ranges of 150-300 m. I subsequently located each of the radioed leverets daily to monitor their survival and movements (Chapter 3). A total of 254 leverets from 103 litters were radio-tagged over the course of this study. Juvenile hares were located visually by following their transmitter signals to their hiding places or sites of mortality. The transmitters usually began to fall off the leverets after 10-14 days, so I attempted to recapture each animal by hand or with a dip net at 10 days of age to reglue the radio. Radios would then usually stay glued to the juvenile hares until they were 3-4 weeks old. At this age, the leverets weighed 300-400 g (Chapter 1), and could be trapped and fitted with light (15-20 g) radio collars (Model TW-2 transmitters, Biotrack) made with nylon webbing, with a foam rubber insert to allow for growth. Using these techniques, I was able to follow juvenile survival from birth to dispersal, loss

of radio (for those leverets which could not be retrapped), or to the end of the summer.

I calculated survivorship curves for the radioed juvenile hares using the Kaplan-Meier procedure (Kaplan & Meier 1958; Pollock, Winterstein & Conroy 1989), a nonparametric estimator which allows censoring of data (due to radio loss or failure, dispersal, or animals living beyond the duration of the study) and staggered entry of animals (Pollock *et al.* 1989). Survivorship curves were compared using the log-rank test (Savage 1956, as described in Pollock *et al.* 1989) for 2-sample comparisons (e.g. between grids, years, or sexes), and using the k-sample test (Peto & Peto 1972, as described by Lee 1980) for comparisons of more than two curves (e.g. among litter groups). I investigated the effects of covariates such as body weight and litter size on survival rates using logistic regression (Cox 1970, described in Lee 1980; SAS PROC LOGIST written by Harrell 1983). I calculated separate regression models with body weight at birth and litter size as the single independent variables and survival as the bivariate dependent variable (0 = dead, 1 = alive), and a multivariate model with both dependent variables. Statistical significance was tested at the  $P = 0.05$  level.

## **RESULTS**

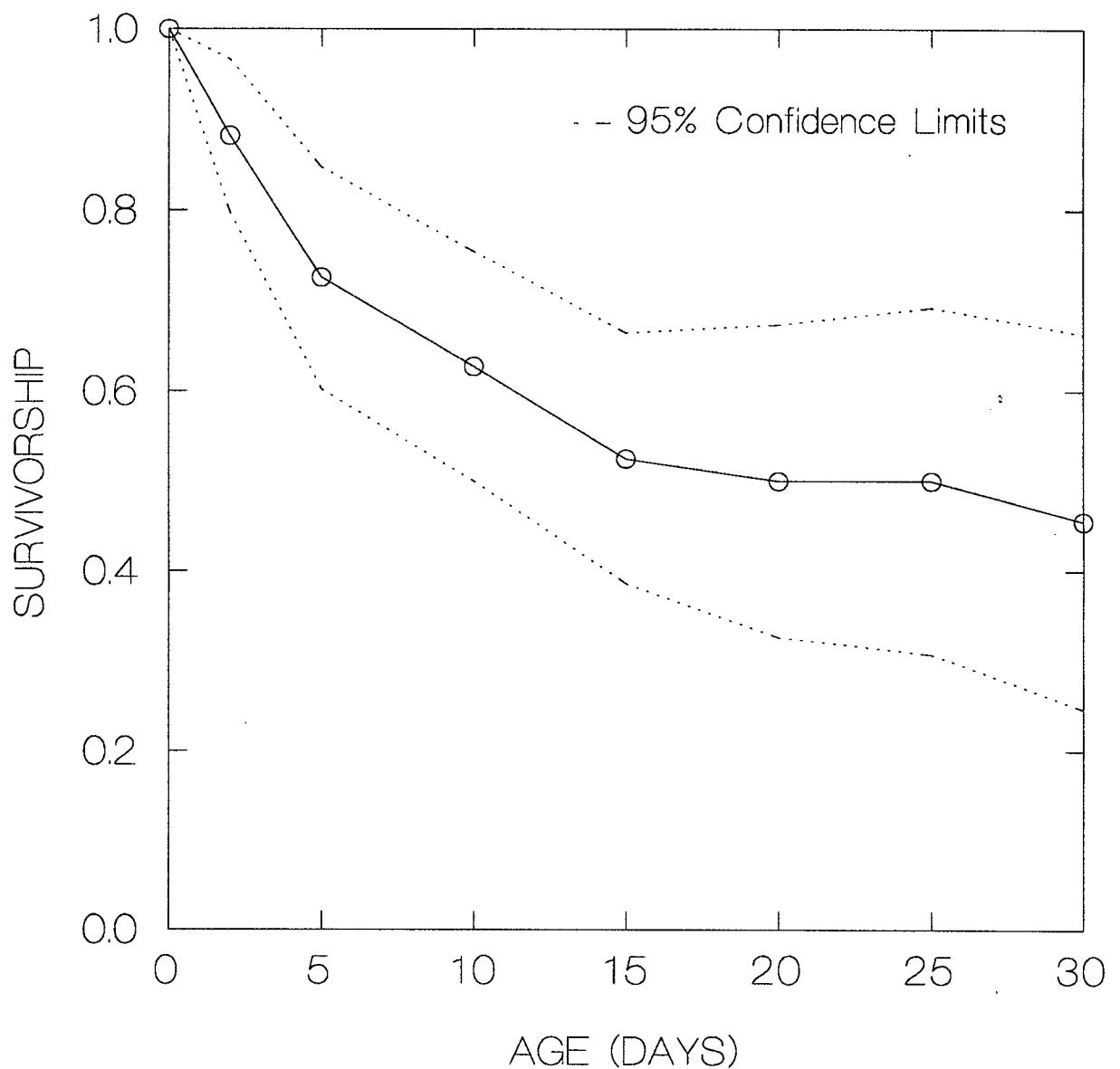
### **Survival Rates of Juvenile Hares**

There were no significant differences between survival rates calculated for juvenile hares in 1989 and those in 1990 (log-rank test,  $0.10 < P < 0.25$ ),

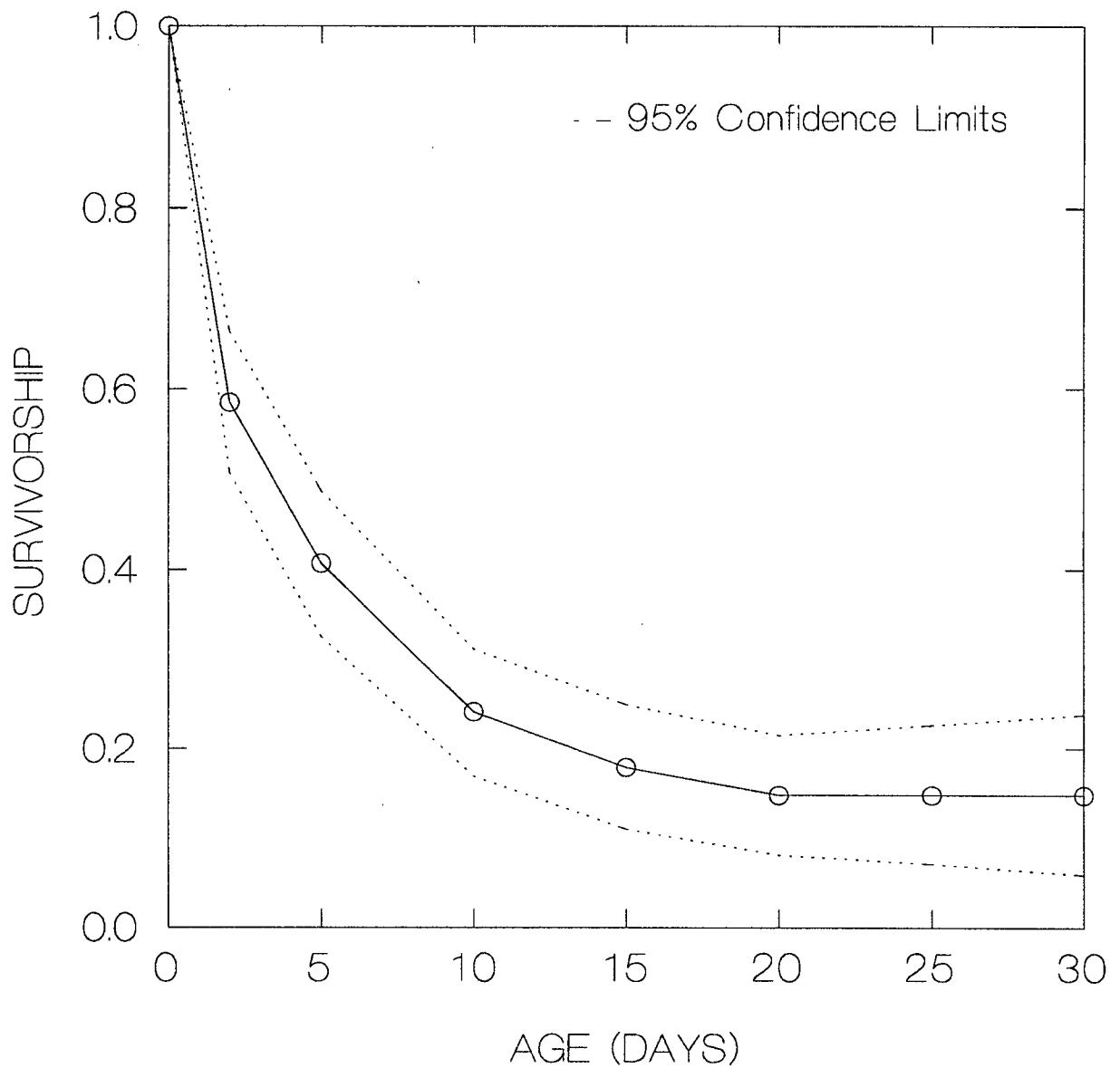
or between males and females (log-rank test,  $0.25 < P < 0.50$ ), based on the survival of radioed leverets. The data were therefore pooled, and survivorship curves were calculated for each litter group on the Food1 grid, and for each litter group on the Control1 grid. Juvenile survival was not significantly different between the food addition and control grid for any of the three litter groups (log-rank test; Litter 1,  $0.50 < P < 0.75$ ; Litter 2,  $0.90 < P < 0.95$ ; Litter 3,  $0.25 < P < 0.50$ ). Survivorship curves are therefore presented for each litter group for both grids combined in Figures 2.1-2.3. After 30 days of age, sample sizes were quite low, and confidence intervals large for each litter, so I restrict further discussion to 30-day survival rates. The survivorship curves of first litter (Figure 2.1, 30-day survival = 0.46) and third litter (Figure 2.3, 30-day survival = 0.43) juveniles were similar, and juvenile survival for these litters was quite high relative to that of second litter juveniles (Figure 2.2, 30 day survival = 0.15; k-test,  $P < 0.001$ ). In all three litters, most of the mortality occurred during the first 10 days of life.

Twenty-seven (10.6%) of the radioed leverets disappeared from the study grids and were never found. Of these, 17 (6.7%) were younger than weaning age, and likely did not disperse. I do not know how many of these missing animals were carried off or had their radios destroyed by predators, and how many had failed transmitters. Missing animals were considered as censored for analysis of survival rates. In order to investigate potential biases caused by censoring missing animals, I calculated survivorship curves treating all missing animals as mortalities, and all as survivors to the end of the study whose radios failed (Figure 2.4). The survivorship curves in Figure

**Figure 2.1.** Survivorship curve for first litter juvenile snowshoe hares (mean birth dates 19-26 May), based on radio-tagged leverets ( $n = 51$ ) on the Food1 and Control1 grids in 1989 and 1990 (sexes pooled).



**Figure 2.2.** Survivorship curve for second litter juvenile snowshoe hares (mean birth dates 22 June - 4 July), based on radio-tagged leverets ( $n = 123$ ) on the Food1 and Control1 grids in 1989 and 1990 (sexes pooled).



**Figure 2.3.** Survivorship curve for third litter juvenile snowshoe hares (mean birth dates 25 July - 8 August), based on radio-tagged leverets ( $n = 77$ ) on the Food1 and Control1 grids in 1989 and 1990 (sexes pooled).

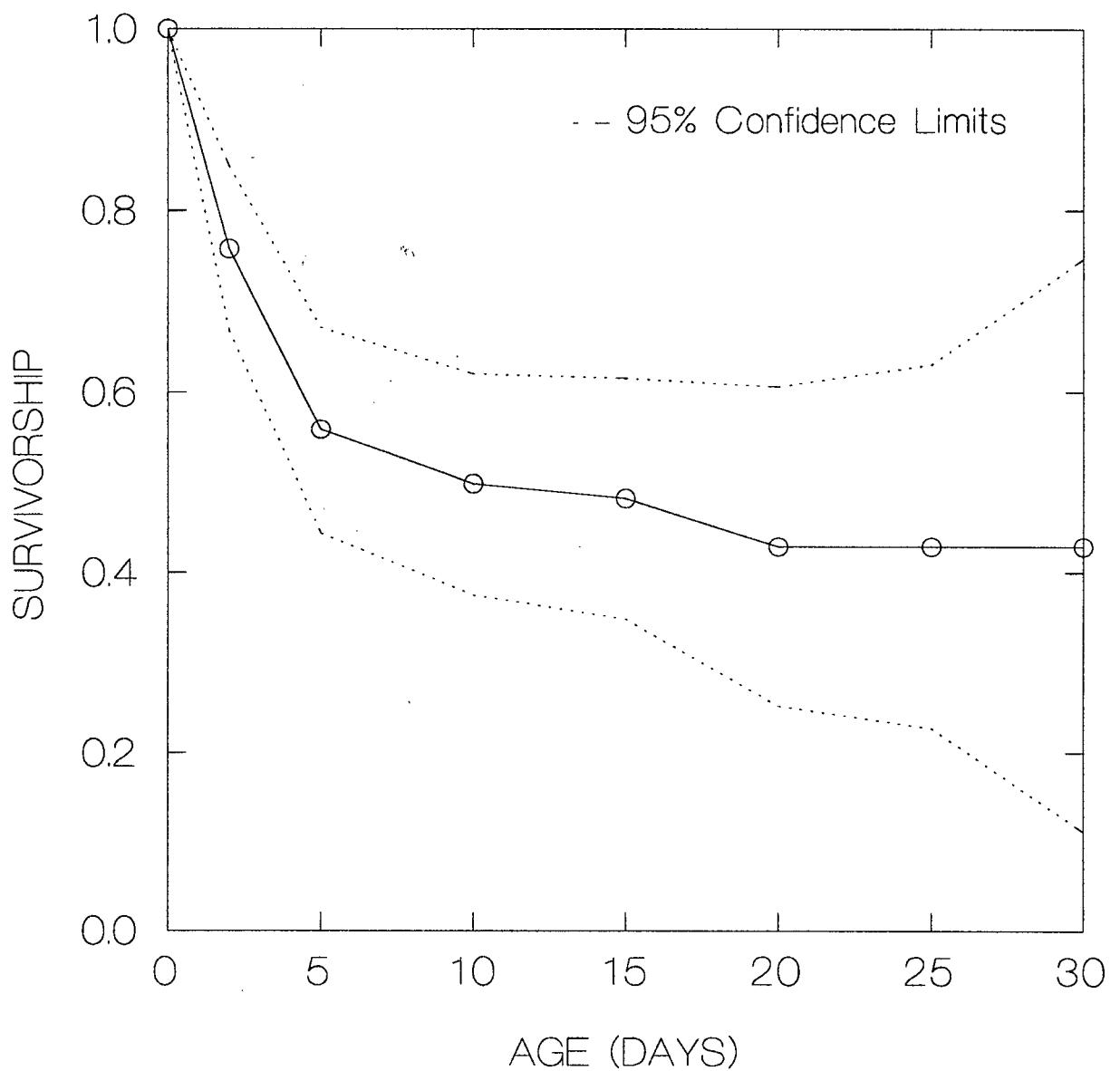
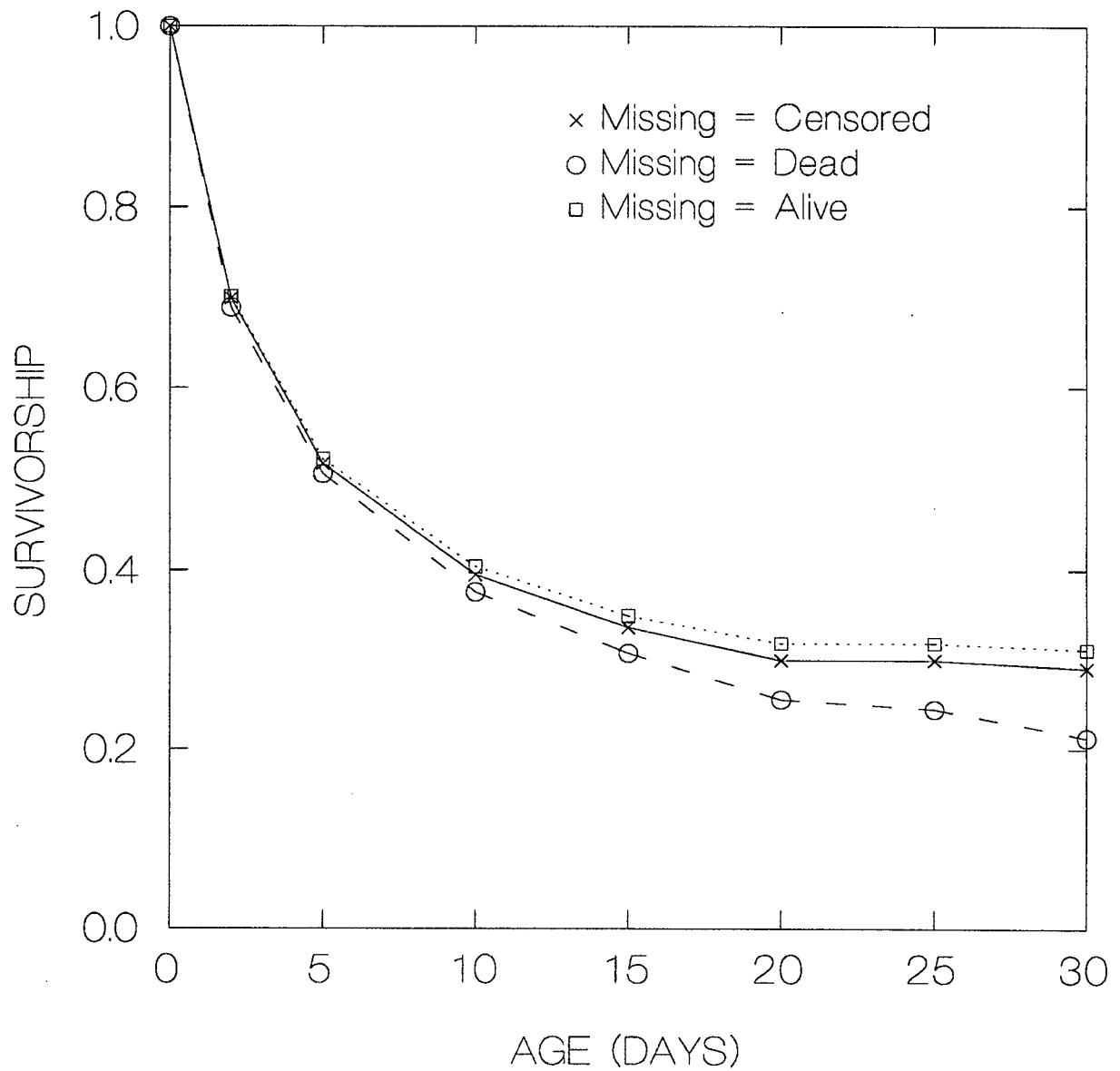


Figure 2.4. Survivorship curves for all radioed juvenile snowshoe hares, with missing animals treated as mortalities, as survivors to the end of the study with transmitter failures, or as censored observations. Little bias was introduced by the method of handling missing animals in the data analysis.



2.4 indicate that little bias was introduced by the method of handling missing animals in data analysis.

Survival of juvenile hares on the Food2 and Control2 grids could be estimated only by an index of survival based on the success rate of retrapping leverets tagged as newborns (Table 2.1). While the retrapping rates were higher on the Control2 grids than the Control1 grid in both years, and higher on the Food2 grid than on the Food1 grid in one year, these differences were not statistically significant in either year (G-tests with Williams correction,  $P > 0.05$ ), suggesting similar survival rates.

### **Proximate Causes of Mortality**

Predation and suspected predation accounted for 82% of the known juvenile hare mortalities. Of the 254 leverets radioed, 170 (67%) died during the time they were being monitored (Table 2.2). The bloodied and usually partially eaten carcasses of 34 (20.0%) of the mortalities were found cached in red squirrel (*Tamiasciurus hudsonicus*) middens or in spruce trees in their middens used for storage. On two occasions, red squirrels were found eating freshly-killed radioed leverets, and on another, a red squirrel was observed carrying a wounded 1-day old juvenile. Another 46 (27.1%) of the mortalities were found cached in spruce trees with no indication of the predator or scavenger which put them there. Several potential predators, including red squirrels, grey jays, and ravens (*Corvus corax*), could have carried dead leverets to trees, but as most carcasses were placed in spots among the upper branches of spruces in the same manner as in midden trees, red squirrels

Table 2.1. Proportions of juvenile snowshoe hares tagged as newborns which were subsequently retrapped on study grids.

Year	Grid	No. of Tagged Newborns	Number Retrapped	Percentage Retrapped
1989*	Food1	91	6	6.6
	Food2	71	8	11.3
	Control1	96	9	9.4
	Control2	35	7	20.0
1990*	Food1	155	14	9.0
	Food2	135	7	5.2
	Control1	146	8	5.5
	Control2	115	16	13.9

\* No significant differences between Food1 and Food2 grids or between Control1 and Control2 grids in either year (G-test with Williams correction, P > 0.05).

Table 2.2. Proximate causes of mortality of radioed juvenile snowshoe hares.

Mortality Factor/ Situation of Recovered Radio	Number	Percentage of Mortalities
Suspected Red Squirrel Kill	34	20.0
Carcass/Radio in Tree	46	27.1
Suspected Ground Squirrel Kill	18	10.6
Unknown Small Predator Kill	31	18.2
Goshawk Kill	6	3.5
Great-horned Owl Kill	2	1.2
Red-tailed Hawk Kill	1	0.6
Exposure	2	1.2
Unknown Cause	30	17.6
<b>TOTAL</b>	<b>170</b>	

seem the most likely agents. The evidence suggests, therefore, that red squirrels are important predators of very young hares.

Eighteen (10.6%) juvenile hares were found mostly eaten in arctic ground squirrel (*Spermophilus parryii*) burrows. Typically, all that was left of the carcass was the peeled-back skin and some bones. Another 31 (18.2%) mortalities were found dead on the ground with bite marks of a small predator, usually on their hindquarters or head. These were likely either red squirrel, ground squirrel, or weasel (*Mustela erminea*) kills, but I was unable to determine the predator. Raptors (Northern goshawk (*Accipiter gentilis*), great-horned owl (*Bubo virginianus*), and red-tailed hawk (*Buteo jamaicensis*)) were known to kill 9 (5.3%) of the radioed hares. Finally, I found 30 (17.6%) of the juveniles dead, with no obvious cause of mortality.

I classified all dead juvenile hares found in red squirrel middens as suspected red squirrel kills, and all found in ground squirrel burrows as ground squirrel kills. However, some of these could have been scavenged by squirrels after they had died of other causes. I located all radioed animals each day, so only high 1-day scavenging rates could have significantly affected my interpretation of scavenged "natural" deaths as predator-killed. To test the efficiency of scavengers, I placed 40 juvenile hare carcasses (stillbirths from previous years) at randomly-chosen grid points on the Food1 and Control1 grids in early June 1991. I attached a small bobbin of thread to the back of each carcass with glue so I could follow the path of any carcasses removed (as used by Boonstra & Craine 1985 with live animals), and put a spot of the epoxy used for radio potting on their backs to simulate a radio

transmitter. On the first day, the carcasses were placed under shrubs and logs in typical hiding places of juvenile hares; on the second day they were placed in the open and cut with a knife to release the smell of blood. On the first day, 4 of the 40 carcasses were scavenged by red squirrels (1 left in a spruce tree next to a midden, and 3 in other spruce trees), and 3 were scavenged by ground squirrels. On the second day, 5 of the 33 carcasses were scavenged by red squirrels (1 left in a midden, 2 in trees next to middens, and 2 in other spruce trees), 2 by ground squirrels, 2 by grey jays (*Perisoreus canadensis*), and 1 by a goshawk. In summary, a total of 23% of the carcasses put out were scavenged within one day of being placed on the grids, compared to 86% of mortalities which I classified as predator-killed during first litter in 1989 and 1990. Only 4 (6%) were left in red squirrel midden areas, compared to 18% of the first litter mortalities I observed. Therefore, while some of the juvenile hares found in trees or in burrows may have been scavenged, it seems likely that most were killed by predators.

### **Potential Biases of Measured Survival Rates**

At least two potential biases could have affected the survival rates which I measured. First, the radio tags attached to the juvenile hares could have attracted predators and increased mortality rates. I controlled for this by only radio-tagging half of each litter, and comparing the subsequent retrapping rates of tagged radioed leverets to tagged unradioed leverets. On the Food1 and Control1 grids, 254 out of 466 (54.5%) juvenile hares born in cages were radio-tagged. Thirty-seven of these juveniles were recaptured in

live-traps, of which 24 (64.9%) were radioed. This was not significantly different from the expected proportion (G-test with Williams correction,  $0.25 < P < 0.50$ ), indicating that radio tags did not markedly affect survival of juvenile hares.

Second, as I chose the nest sites for hares born in my cages, I may have increased their mortality rates in this way. I attempted to analyze this in two ways. First, I considered that if caging females had no effect on subsequent juvenile survival, then the relative frequencies of untagged juveniles to juveniles tagged at birth that were captured in live-traps should equal those of uncaged to caged litters born on the grids. I estimated the number of uncaged litters born on each grid by multiplying the observed minimum number of females alive on each grid during the breeding season by the observed pregnancy rates, and subtracting the number of caged females for each litter group. The ratio of uncaged to caged litters was 5.9 to 1 (1139:193) for all four grids in both years. Juvenile hares began to disperse soon after weaning (Chapter 3), so I calculated the ratio of untagged to tagged juveniles in traps with hares weighing less than 500 g only. This ratio was 4.6 to 1 (161:35), which is not significantly different from the ratio of uncaged to caged litters (G-test with Williams correction,  $0.25 < P < 0.50$ ). This suggests that caging female hares did not markedly affect subsequent juvenile survival.

I also constructed a simple model of hare demography to examine whether the early juvenile survival rates that I observed were realistic based on the observed pattern of population change between 1989 and 1990 at

Kluane. I used the rates of reproductive output (Chapter 1) and juvenile survival that I observed in this study, and rates of adult summer and overwinter survival calculated on the Kluane Project control (Sulphur) and food addition (Gravel Pit) grids (C. J. Krebs, unpublished data) to calculate the expected population trend (Table 2.3). Using the minimum and maximum adult survival rates measured on the Kluane Project grids in 1989 and 1990 as estimates of adult and older juvenile survival on all grids, 1990 populations would be expected to be 0.6-1.4 times those in 1989 if the early juvenile survival rates I observed were unbiased. The observed populations in 1990 on the four grids were 0.9, 0.9, 1.2, and 1.9 times those in 1989, based on Jolly-Seber population estimates, again suggesting that caging of female hares did not adversely affect juvenile survival.

### **Factors Affecting Juvenile Survival**

One of the assumptions of the Kaplan-Meier procedure for survival estimation is that the survival of all radioed animals is independent. Correlated survival of radioed individuals would not bias the survival rates, but would reduce the observed variance (Pollock *et al.* 1989). It seems unlikely that the survival of littermates is independent for species with extended post-natal care. Snowshoe hare litters stay together in the nest for only 1-7 days (mean = 2.7 days; Chapter 3), but 70% of all observed mortality occurred during the first 5 days of life. To examine the independence of littermate survival, I compared the observed distribution of the proportion of radioed littermates in each litter surviving, with that expected by chance if

Table 2.3. Demographic parameters used in a simple model of snowshoe hare populations on study grids at peak numbers.

Parameter	Observed Values	Source
<b>Adult Survival Rates</b>		
May-October	0.885-0.970 / 30 days	Kluane Project (unpublished data)
November-April	0.865-0.925 / 30 days	Kluane Project (unpublished data)
<b>Juvenile Survival Rates to Sept.</b>		
First Litter	0.273	This study
Second Litter	0.148	This study
Third Litter	0.429	This study
<b>Reproductive Output<sup>a</sup></b>		
First Litter	3.39 juv. / ad. fem.	Chapter 1
Second Litter	5.62 juv. / ad. fem.	Chapter 1
Third Litter	3.42 juv. / ad. fem.	Chapter 1

<sup>a</sup> Reproductive Output = (Mean Litter Size) (Pregnancy Rate) (1 - Stillborn Rate).

survival was independent. Expected frequencies were calculated using the observed overall survival rate to 14 days of age (after this point, most transmitters fell off animals I was unable to recapture), and calculating the proportion of radioed littermates expected to survive per litter based on the binomial distribution (as in Boutin, Moses & Caley 1988). More littermates all survived or all died as a unit than expected by chance if littermate survival were independent (Figure 2.5; G-test with Williams correction,  $P < 0.001$ ). In 49 out of the 96 litters (51%), no radioed juveniles survived to 14 days of age. (Transmitters fell off some of the young before they were 14 days old in 7 litters, so only 96 of the 103 litters are included in this analysis). If only juvenile survival from 5-14 days of age is considered, after over 90% of the litters had split up, then the observed and expected frequency distributions of proportions of littermates surviving were not different (Figure 2.6; G-test with Williams correction,  $P = 0.95$ , classes with fewer than 5 expected observations pooled). These analyses suggest that survival of littermates is not independent before the breakup of the litters, but may be so after this point.

Litter sizes of hares on my four study grids varied from 1 to 9, and birth weights of the juvenile hares ranged from 28 to 114 g in 1989 and 1990 (Chapter 1). The two factors were significantly negatively correlated ( $r = -0.49$ ,  $P < 0.001$ ), with hares in smaller litters tending to be larger at birth. Survivorship curves of juvenile hares by litter-size class (Figure 2.7) and birth-weight class (Figure 2.8) suggest that leverets from larger litters and of smaller body size survive more poorly than those from small litters of large-

Figure 2.5. Observed and expected frequency distributions of proportions of radioed littermates surviving to 14 days of age. Expected frequencies were calculated assuming independent littermate survival and a survival rate of 0.35. More littermates all died or all survived as a unit than expected by chance (G-test with Williams correction,  $P < 0.001$ ).

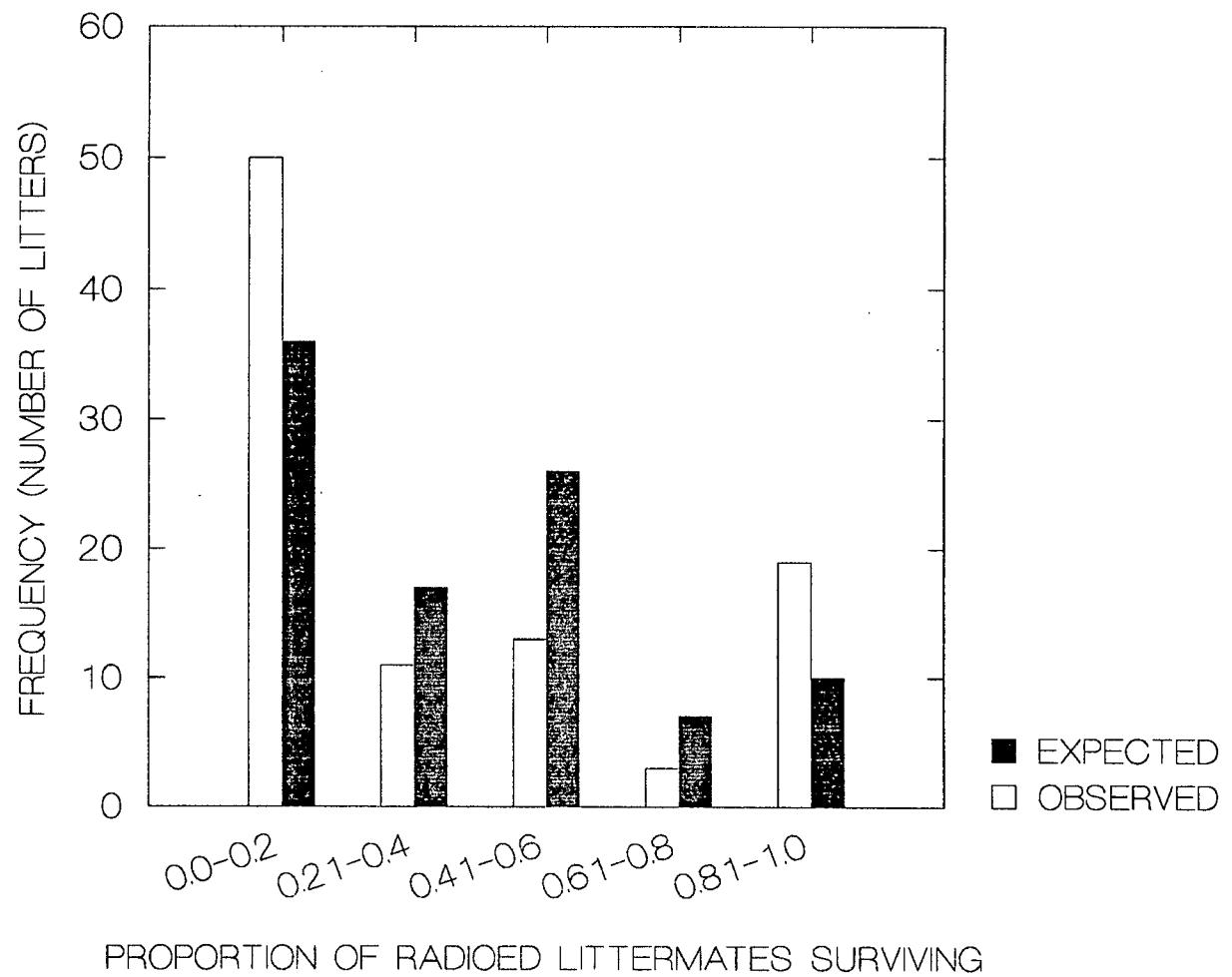
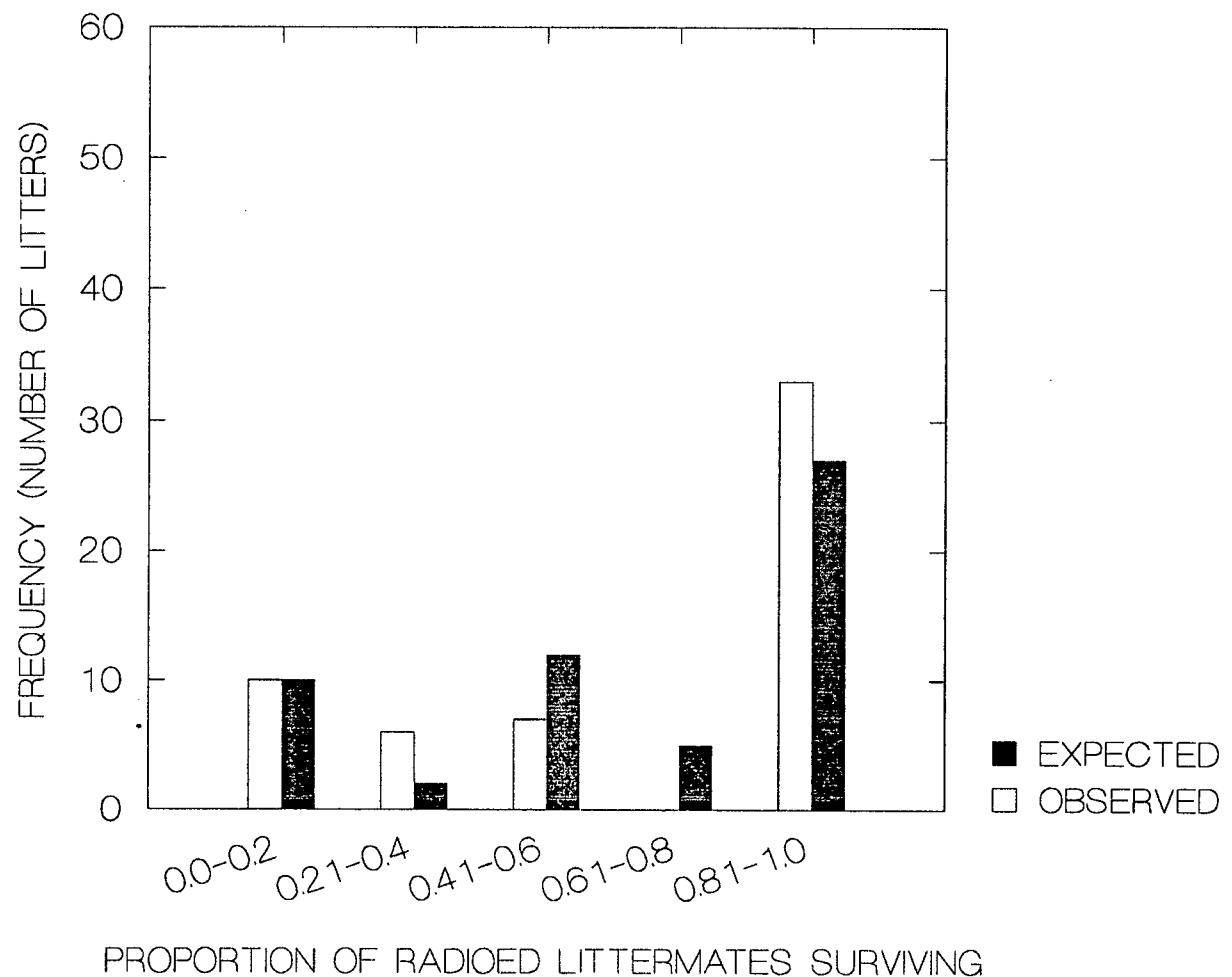
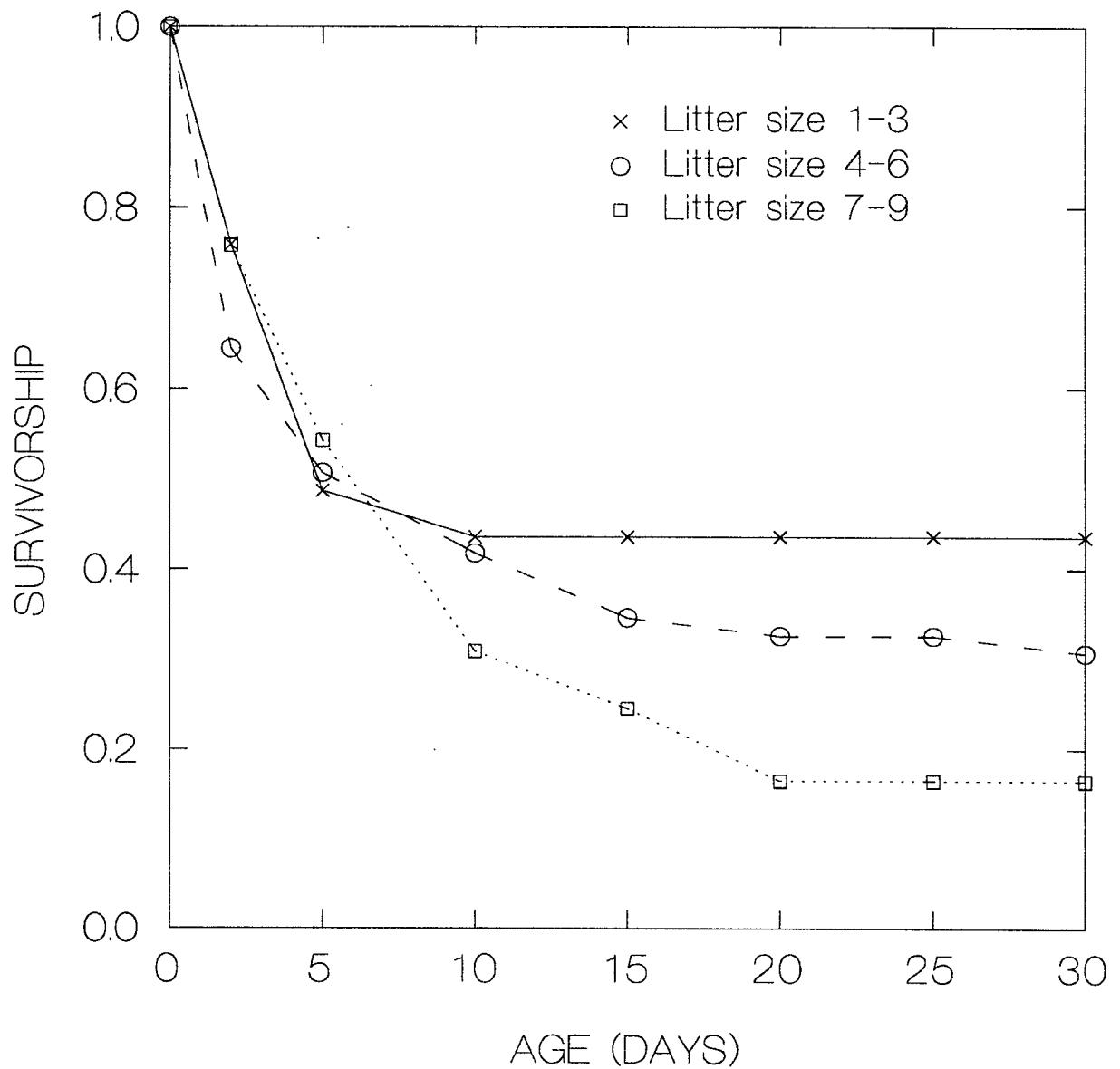


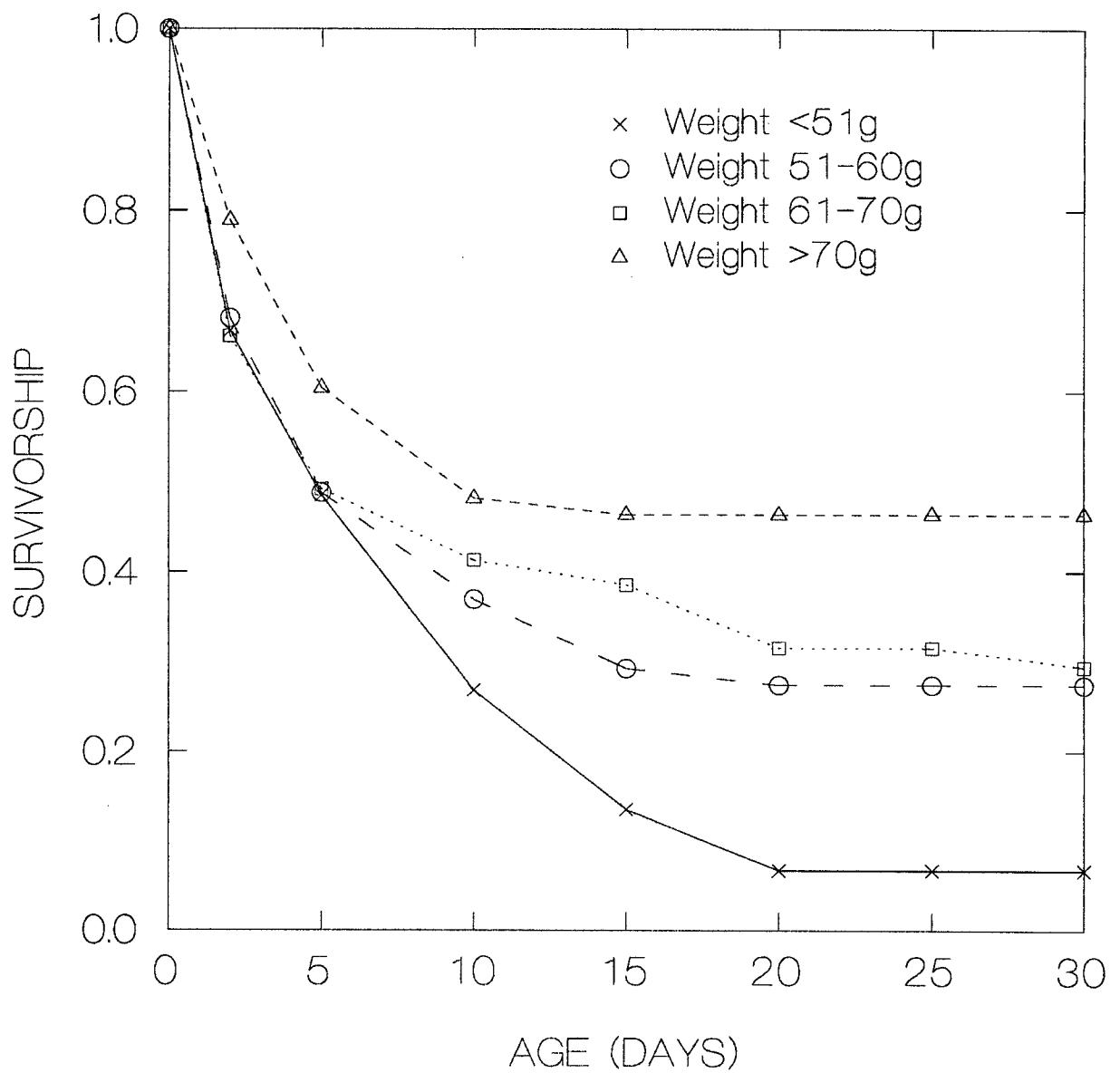
Figure 2.6. Observed and expected frequency distributions of proportions of radioed littermates surviving from 5 to 14 days of age. Expected frequencies were calculated assuming independent littermate survival and a survival rate of 0.67. Expected and observed frequencies were not different than expected by chance (G-test with Williams correction,  $P = 0.95$ ).



**Figure 2.7.** Survivorship curves of juvenile snowshoe hares by litter size class.



**Figure 2.8.** Survivorship curves of juvenile snowshoe hares by birth-weight class.



sized juveniles. Logistic regression models considering litter size and birth-weight as the single independent variables indicated that both factors significantly affected 30-day survival rates ( $P < 0.05$ ). However, when both variables were entered in a multivariate logistic regression model, only body weight at birth was significant ( $P = 0.01$ ). Therefore, while litter size *per se* was not significantly related to survival, larger litters generally were of smaller-sized leverets, which had lower survival rates than juveniles of larger body size. A logistic regression model considering the effects of both variables on survival to 5 days of age indicated that neither significantly influenced survival ( $P > 0.15$ ).

## ***DISCUSSION***

The results of this study indicate that survival of juvenile snowshoe hares to weaning is low, especially for those born in second litters. There are two reasons why rates of predation on leverets by small predators may have been higher for second litter juveniles. First, hares produced larger litters of generally smaller-sized offspring in the second litter. Small predators such as squirrels may have responded functionally to the increased abundance of newborn hares and actively foraged for them. Second, the late-June birth dates of second litter hares correspond to a period of increasing independence of juvenile red squirrels and ground squirrels (S. Boutin, personal communication). Thus the number of potential predators of leverets at this time was also greater than at first litter in May.

Hare populations were at peak abundance during both years of my field work, so this study does not clarify the importance of changes in early juvenile survival to population trends. However, these results do suggest mechanisms by which changes in early survival rates could occur over the hare cycle. Predation on juvenile hares by small mammalian predators appears to be the most important cause of mortality. These predation rates could increase as hares approach peak numbers in two ways: 1) small predators could show Type III (Holling 1959) functional responses to the increased availability of young hares as prey, as do some larger predators to older hares (Keith *et al.* 1977), or 2) functional responses of larger predators to hare abundance could reduce predation pressure on their other prey species, such as red squirrels and ground squirrels, and allow them to increase in numbers, thereby increasing predation rates on juvenile hares. In Scandinavia, a functional dietary shift to voles by predators during microtine cyclic peaks may reduce predation pressure on mountain hares (*Lepus timidus*) and black grouse (*Tetrao tetrix*) and allow their populations to increase (Angelstam, Lindström & Widén 1984). Data on the population responses of alternative prey species such as squirrels to the snowshoe hare cycle are thus far inconclusive. Studies of juvenile hare survival, and of the diets and numerical trends of small predators of leverets over the hare cycle, would be necessary to investigate the effects of predation on recruitment trends.

Indices of early juvenile survival calculated from live-trapping (e.g. Keith & Windberg 1978) may be confounded by changing dispersal rates.

Juvenile hares begin to disperse soon after weaning (Chapter 3), and dispersal rates are highest at the peak and early decline phases of the cycle (Windberg & Keith 1976; Boutin *et al.* 1985). While lower juvenile survival at the cyclic peak would lower the indices of survival, increased movement of dispersing hares through study grids at the same time would elevate them. Therefore, the lack of correlation between early juvenile survival and population changes seen in Alberta (Keith & Windberg 1978) may not accurately reflect the importance of survival to weaning to overall demographic trends.

I observed no differences between early juvenile survival rates on the control and food addition grids. This result is consistent with my findings that reproductive output was the same on food-supplemented and control grids as well (Chapter 1). During peak hare years at Kluane, there is no evidence that food limited the rate of recruitment to weaning. This is contrary to the results of Vaughan & Keith (1981), who found that both reproductive output and juvenile survival were higher in captive hare populations with supplemental food than in control populations. The densities of hares in Vaughan & Keith's experimental populations were from 1.5 to 7.5 times the highest observed on my study grids, but it is unknown whether this could account for the differences in our results.

The importance of predation on leverets by small mammals such as squirrels was unexpected, and has not been previously reported. There are several published reports of weasels killing young hares (Severaid 1942, Rongstad & Tester 1971), and one of a grey jay killing a 1-day old captive

hare (Graf & Sinclair 1987). Some of the hare radios that I found in trees could have been carried there by avian predators such as grey jays, but most were complete or partially-eaten carcasses with bite marks visible. The hare carcasses scavenged by grey jays in my scavenging experiment were both eaten on the ground, and the bones were left pecked clean. There have been several published accounts of ground squirrel predation on other vertebrates. Boonstra, Krebs & Kanter (1990) suggested that arctic ground squirrels may actively forage for collared lemmings (*Dicrostonyx kilangmiutak*) in the Northwest Territories. This study is the first report suggesting that both ground squirrels and red squirrels may be opportunistic or active predators on young snowshoe hares. I did not find any evidence of large mammalian predators such as lynx (*Lynx canadensis*) or coyotes (*Canis latrans*) killing juvenile hares, but as my radios only had a range of 150-300 m, it is unlikely that I would have found dead hares carried off by wider-ranging carnivores. I only lost contact with 27 (10.6%) of the radioed juvenile hares, so even if all of these represented predation by large predators, they would still not be a large fraction of the early juvenile loss.

The survival of individual juvenile snowshoe hares was not independent between littermates, a result also found by Boutin, Moses & Caley (1988) with muskrats (*Ondatra zibethicus*). The correlation between littermate survival could be due either to predators actively searching out and killing all the juvenile hares in a litter once one was located, or to female hares abandoning or not protecting their litters. The evidence suggests that the former was the case. While juvenile hares were still together in the nest,

radioed littermates were often killed by predators on the same day--70% of known mortalities occurred during the first 5 days after birth. Young hares died in their nest with no sign of predation in only four cases. Once the litter broke up as a unit, at 1-7 days of age, survival of young was independent, which suggests that it was more difficult for predators to locate all of the young in a litter. The logistic regression indicated that litter size and birth weight had no significant effects on survival to 5 days of age. If a predator located juveniles together in their nest, they may have been easily killed as a unit regardless of their body size, whereas juvenile size and mobility may have been more important in determining success of avoiding predation once the leverets were independent.

Life history theory predicts that there should be trade-offs between litter size, body size of offspring, and individual survival (Lack 1947, Williams 1966, Stearns 1976). Litter size should be adjusted such that the maximum number of young survive to maturity (Lack 1947, Charnov & Krebs 1974). Experimental evidence for the existence of these trade-offs is mixed. Studies on birds have suggested negative (review in Klomp 1970), positive (Högstedt 1980), and no relation (Nur 1984) between clutch size and juvenile survival. There have been very few studies of the relationship between litter size and juvenile survival in wild mammals. Morris (1986) suggested that juvenile survival was highest in intermediate litter sizes of *Peromyscus leucopus*, based on a nest-box study in Ontario. He found juvenile survival to be lowest at very large litter sizes, and marginally lower at smaller litter sizes. Morris (1986) argued that species with frequent

iterated reproduction should reduce investment in litters smaller than the optimum size in favor of larger litters *in utero*, which could explain lower survival rates of small litters. However, Boutin, Moses & Caley (1988) found no correlation between litter size and juvenile survival of muskrats.

This study is the first to find evidence of a trade-off between litter size and juvenile survival in a wild mammal. Juvenile survival, as measured here, represents only survival to the age of weaning, and not to sexual maturity. It is not known whether there is a different pattern of survival among juveniles from different litter sizes beyond the age of weaning that would change the observed relationship between litter size and juvenile survival.

These data indicate that smaller-sized juveniles tend to come from large litters, and that they are more vulnerable to predation than are larger-sized juveniles. As a result of this trade-off between litter size and juvenile survival, female hares recruit approximately the same number of offspring to weaning age over all observed litter sizes (Table 2.4). Also, although the survival rate of juveniles from small (1-3) litters is almost three times that of juveniles from the largest (7-9) litters, the probability that at least one offspring survives per litter is approximately the same for all litter sizes as well. Optimum litter size is not likely to be the same in each of the litter groups during the summer, due to changes in predation pressure and the nutritional states of females. Within each litter group, there was too little variance in litter sizes, and my sample sizes were insufficient, to discern separate optimal litter sizes for each litter group, or to determine what

Table 2.4. Summary of juvenile survival rates, recruits per litter, and probabilities of total litter failure by litter size for snowshoe hares on study grids.

Litter Size	n	Survival Rate to 30 days of age	Mean Number of Survivors per Litter to 30 days of age <sup>a</sup>	Percent of Litters with no Survivors to 14 days of age <sup>b</sup>
1-3	25	0.44	1.13	60.0
4	32	0.33	1.32	45.2
5	17	0.27	1.35	52.9
6	13	0.34	2.04	38.5
7-9	16	0.17	1.24	50.0

a No significant difference between observed and expected mean number of survivors (G-test with Williams correction,  $0.25 < P < 0.50$ ). Expected values calculated based on relative frequency of litter-size classes.

b Probability of total litter loss calculated with juvenile survival rates to 14 days of age, because after this age, transmitters fell off many of the juveniles which were not recaptured.

parameter, if any, was maximized (i.e. number of juveniles surviving per litter vs. the probability that at least one offspring survives). For example, 81% (35/43) of radioed second litters were of 4-7 offspring. Over these four litter sizes, the probability of total litter loss varied only between 56% and 63%. Only four litters of less than 4 young were born during second litter, but they contributed a mean of 0.35 recruits per litter relative to 0.87 recruits per litter for larger litters sizes ( $n = 39$ ). These sample sizes are obviously too low for small litter sizes to draw any firm conclusions, but they suggest that fewer young may be recruited from small litters during periods of high predation pressure. Experimental manipulation of litters would be necessary to have an adequate range and sample of different litter sizes in order to determine whether different optimums exist for the different litter groups. As female snowshoe hares apparently readily accept and nurse strange young (Chapter 3), they would be ideal subjects for such experiments.

I found no evidence in this study that female hares invested less in small litters, as suggested by Morris (1986). Due to the high probability of total litter loss, it seems unlikely that it would be advantageous for mothers to abandon litters of any size in favour of potentially larger future litters. Boutin, Moses & Caley (1988) reached the same conclusion based on their study of muskrat survival. Post-partum oestrus and multiple litters per season (as exhibited by many small mammals) are often seen as mechanisms of spreading the risk of complete litter loss over several reproductive bouts (Morris 1986; Boutin, Moses & Caley 1988). Reproductive success of

snowshoe hares at peak densities may be largely dependent on their litters surviving the lottery of predation.

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## **CHAPTER 3: EARLY MOVEMENTS AND DISPERSAL OF JUVENILE SNOWSHOE HARES**

### **INTRODUCTION**

Little is known about the movements of juvenile snowshoe hares (*Lepus americanus*) before the age of weaning, or about the timing of natal dispersal. Snowshoe hares do not make nests (Severaid 1942; Graf & Sinclair 1987), and adult females apparently only nurse their young once per day (Rongstad & Tester 1971; Graf & Sinclair 1987), so hare litters are difficult to locate in the field. The precocial young are born fully-furred, and they are mobile with their eyes open within an hour after birth (Severaid 1942).

Only three published studies have addressed the behaviour of juvenile snowshoe hares; two of these were based on observations of captive hare litters (Severaid 1942; Graf & Sinclair 1987). The other was based on the movements of four radioed juvenile hares from a single litter (Rongstad & Tester 1971). The following pattern emerges from these few data. Juvenile hares stay together at their birth-site for 1-4 days (Severaid 1942; Rongstad & Tester 1971). When the litters break up, the leverets then find hiding places under vegetation within the female's home range (Rongstad & Tester 1971). Graf & Sinclair (1987) found that juvenile hares often hid together with other juveniles, both littermates and juveniles from other litters, in their pen. The home ranges of the leverets observed by Rongstad & Tester (1971) rapidly increased in size to equal that of their mother by 8 weeks-of-age. Until weaning at 25-28 days (Severaid 1942), juvenile hares gather near

their birth-site each evening shortly after twilight, where they are joined by their mother for a short nursing period of 5-10 minutes (Rongstad & Tester 1971; Graf & Sinclair 1987). Adult females may nurse their last litter of the season for longer than 28 days (Severaid 1942; Rongstad & Tester 1971).

The timing of dispersal by juvenile snowshoe hares is not known. In Alberta, Windberg & Keith (1976) found that the first juveniles appeared in traps on a removal grid in late June each year, about 5-6 weeks after the mean date of parturition on adjacent control grids. Boutin (1984a) found that 30% of recruits to a control grid with radioactive-marked females were immigrants. These two studies suggest that juveniles may begin dispersing during the summer at an early age.

The purpose of this study was to investigate the early movements and timing of dispersal of juvenile snowshoe hares in the wild. It was conducted in conjunction with a study of hare reproduction (Chapter 1) and juvenile survival (Chapter 2), as a part of the Kluane Boreal Ecosystem Project, an ongoing study of the snowshoe hare cycle and boreal community organization. My objectives were to 1) examine the pattern of movements of juvenile snowshoe hares before weaning, 2) determine the timing of natal dispersal and whether or not a sex-bias exists, and 3) determine whether the observed pattern of maternal-juvenile relations was consistent with the published reports.

Snowshoe hare populations undergo periodic fluctuations in abundance throughout the North American boreal forest, with peaks occurring each 8-11 years (Elton & Nicholson 1942). Hare populations in the

Kluane region reached peak densities in 1989 and 1990, and began to decline during the winter of 1990-91 (C. J. Krebs, unpublished data). The two years of this study, 1989 and 1990, thus coincided with high hare numbers. I used control and experimental grids established by the Kluane project in this study.

## METHODS

The study area and general methods were the same as those described in Chapters 1 and 2.

Radioed juvenile hares were relocated daily by following the radio signals and visually observing each animal. If the juveniles fled when approached, I measured their flushing distances from the observer to the point where the animal was first seen. At 10-14 days of age, I attempted to recapture each radioed leveret by hand or with a dip net to re-glue its radio. Once the leverets reached 3-4 weeks old, they began to enter live-traps. At this time, I fitted them with small radio collars weighing 15-20 g, made of nylon webbing with a foam rubber insert to allow for growth. These radios (transmitter Model TW-2, Biotrack) had a range of 300-1000 m, and a battery life of about 6 months. Juvenile hares were followed until they died, their radios fell off (for those which I could not re-trap), or they dispersed and I lost radio contact with them.

During the summer of 1990, in collaboration with C. Bergman, five newly-born hare litters were observed from blinds for a total of 91.5 hours, to

determine the timing and duration of nursing sessions, and the extent of parental attendance to the young.

## **RESULTS**

I found no significant differences in the movements and timing of dispersal between juvenile hares on the food grids and those on the controls (Mann-Whitney U-test,  $P < 0.05$ ), and so I pooled the data for further analysis.

### **Pre-dispersal Movements**

A total of 254 juvenile hares from 96 litters were radio-tagged during the summers of 1989 and 1990. Littermates stayed together at the "nest" site for 1-7 days; the mean number of days to litter break-up was  $2.7 \pm 1.7$  (S.D.) days from birth ( $n = 71$ , disregarding litters in which all the radioed juveniles were killed before litter break-up). The break-up of some litters may have been associated with the disturbance of being handled (25 litters broke up after only 1 day), or with the discovery of the nest by a predator (18 litters broke up on the same day that one of the juveniles was killed). However, the break-up day of litters which may have been disturbed by predators ( $2.3 \pm 1.5$  days,  $n = 18$ ) was not significantly different from that of litters in which all of the radioed juveniles survived to break-up ( $2.9 \pm 1.8$  days,  $n = 53$ ).

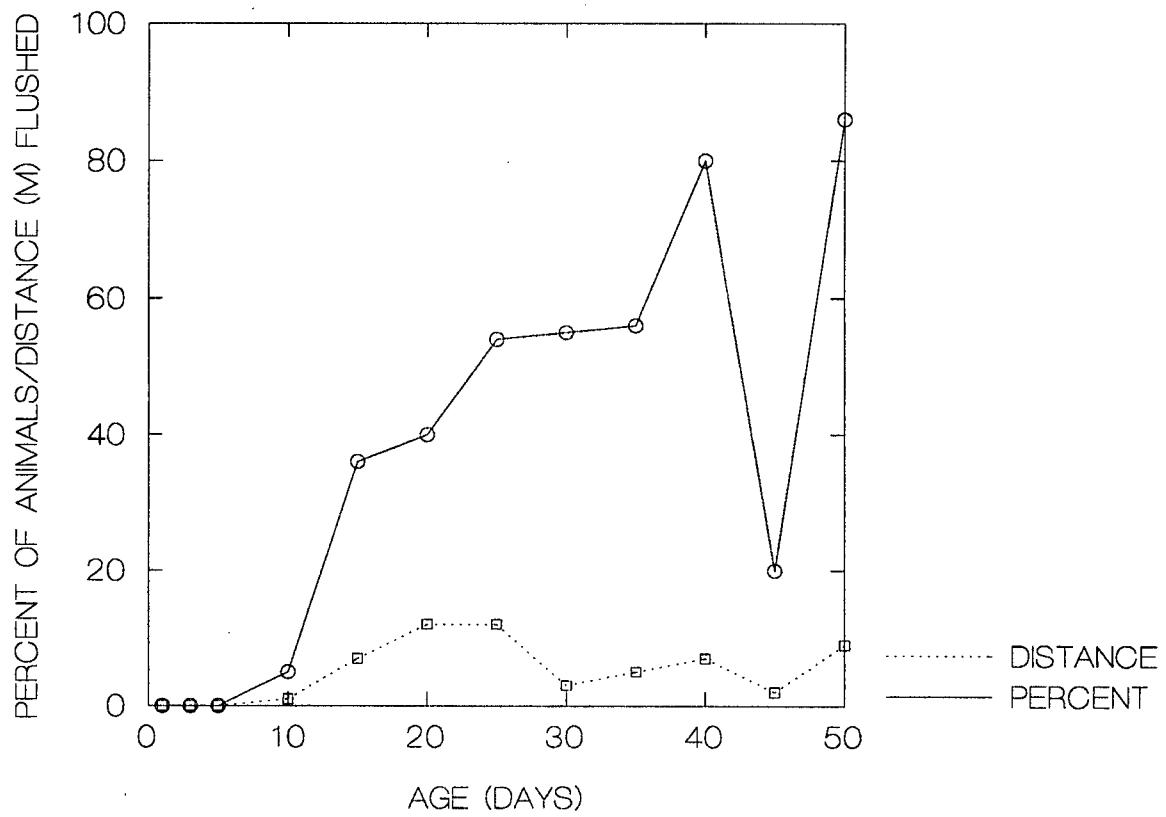
After litter break-up, the individual leverets generally found separate well-concealed hiding places under shrubs (46% of observations), in clumps of grass or herbs (10%), under logs (19%) or in deadfalls (17%). The leverets

mostly stayed alone after leaving the nest. Only 1.6% (29 of 1815 observations) of juvenile hares located out of their nests were with other juvenile hares; 18 of these were hares 5 days or younger. On one occasion, a litter of three 7-day old leverets regrouped at their sheltered nest on a rainy day, 4 days after leaving it. On another, a radioed leveret left its nest at 3 days of age, and was found in the nest of another female about 70 m away on its fourth, fifth, and ninth days, with juveniles 3 days younger than itself.

Young juvenile hares seldom move from their hiding places during the daytime. During four continuous days of observing a litter which had broken up after 1 day, C. Bergman (unpublished data) found that the two radioed leverets (1-4 days old) did not move at all from their individual hiding places on two of the days. On one of the days, only one of the two moved (twice, each time 2-3 m to a new shrub), and on the fourth day, both leverets moved to new hiding places once during the day. Radioed juvenile hares were often found in the same hiding places on consecutive days--one was located under the same log for seven days in a row (5-11 days old). When approached, most radioed hares remained motionless in their hiding spots up to the age of 10-12 days (Figure 3.1). Most could easily be caught by hand at this age. After this point, many animals would not allow the observer to walk closer than 5-10 m before flushing from their hiding places.

The daily locations of radioed hares were insufficient for calculating juvenile home ranges, because the sizes of the home ranges increased rapidly as the leverets grew. However, I calculated the mean distance of all radioed juveniles from their nest sites at each age as an index of changes in mean

**Figure 3.1.** Flushing distances of radioed juvenile hares and percent of animals which flushed from their hiding places when approached (1989 and 1990 data combined).



home range size. Juvenile hares moved progressively farther from their nest sites up to the age of about 20 days, after which the extent of their movements stayed about the same (mean distance from nest site =  $76.0 \pm 46.9$  m (S.D.)) to 35 days of age (Figure 3.2). Leverets older than 35 days which did not disperse, began to travel considerably farther from their nest sites (mean distance =  $134.0 \pm 63.7$  m).

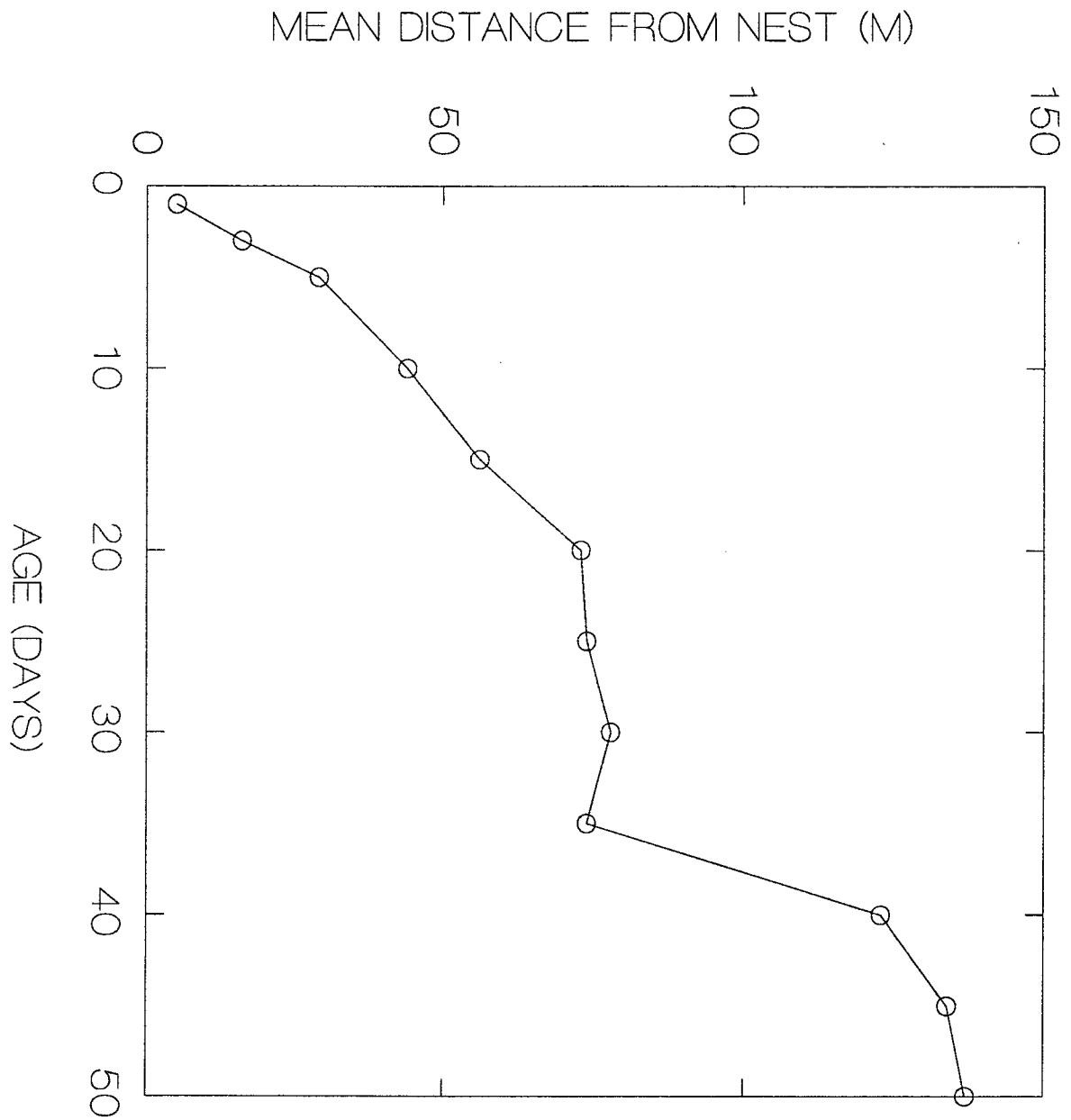
### **Maternal-Juvenile Relations**

I observed a female hare giving birth to her litter on only one occasion. The female sat up straight on her hind legs, and then with her front feet often off the ground, she bent forward and began rapidly licking the young as they emerged. In a period of 15 minutes, the female gave birth to 6 young. The litter then nursed for a period of 5 minutes while the female licked the fur of the newly-born leverets. After nursing, the mother hopped to another corner of the cage and did not return to the young. Within 20 minutes, the fur of the newborn hares was mostly dry, their eyes were open, and they were able to crawl around into a pile.

All observations of female nursing behaviour were made by C. Bergman (unpublished data) during 6 nights at the nest of a single female, when her 3 young were 1-5 and 9 days old. The pattern was the same each night--the mother came and nursed her litter for about 10 minutes between the hours of midnight (about the end of twilight) and 0110. On four of the nights, the juvenile hares gathered near the nest site about 30 minutes before nursing with no apparent solicitation from the female. On two nights,

**Figure 3.2.** Mean distances of radioed juvenile snowshoe hares from their nest sites in relation to age, not including animals which dispersed (1989 and 1990 data combined).

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however (juveniles 4-5 days old), the mother hopped through the area where the individual young were hidden (39-42 m from the nest, and 30 m from each other), and made a repeated chirping vocalization before leaving the area again. The juvenile hares moved towards the nest after this, and were joined by the adult female 20-30 minutes later for nursing. No nursing of young was observed at any other time of the day during the 91.5 hours of nest observations.

Females varied in the extent of maternal defense of their offspring. Mothers were never seen at the nest sites (except for nursing) at three of the five nests observed. At the other two nests, however, the females generally stayed within 30 m of the nest, and vigourously chased all red squirrels (*Tamiasciurus hudsonicus*) and ground squirrels (*Spermophilus parryii*) from the area while the young remained at the nests. Females frequently responded to the alarm cries of juvenile hares being handled by rapidly approaching the observer to within 1-2 m, making loud stamping noises with their hind feet, and clicking their teeth.

Female hares stopped nursing their first and second litters of the season 24-28 days after birth. However, at least some females continued nursing their third litters longer than this. In 1989, I conducted a mid-September trapping session and found females still nursing their third litters 29 (2 females), 31 (2 females), 38 (3 females), and 40 (4 females) days after parturition.

## **Dispersal of Juvenile Hares**

I defined dispersal date as the day on which the juvenile hare moved more than 150 m (the distance to the next line of live-traps) from its mother's known home range (the area encompassing the live-traps in which she was caught) and did not return. Due to the limited range of the juvenile hare transmitters, I was often unable to relocate radioed hares once they dispersed off the grids, despite intensive searches of the areas within 500 m of the last locations. As a result, although I was able to determine the dates of disappearance of many juvenile hares from their natal ranges, I often could not be sure whether these animals had dispersed or had been carried off by predators. I was able to ascertain the ages of natal dispersal of four juvenile hares, all from the first litter of the year. Three males left their mothers' home ranges at the ages of 32, 36, and 42 days, and one female dispersed at 43 days of age. Another first litter female moved 500 m from her natal range at 94 days of age, but returned 9 days later. Based on live-trapping data, I was also able to determine that four juvenile males dispersed at <41 days (third litter), <44 days (second litter), 50-70 days (second litter), and <65 days (first litter), and that two females dispersed at <51 days (first litter) and <61 days (first litter).

There were too few known dates of dispersal to test for a sex bias in the timing of dispersal. However, I calculated three different indices of persistence within natal home ranges to look for differences between the sexes (Table 3.1). For radioed juvenile hares, I calculated the mean age at last location within the mothers' home ranges for all juveniles wearing radios

Table 3.1. Indices of timing of natal dispersal for male and female juvenile snowshoe hares on study grids (sample sizes in parentheses).

	Mean Age at Last Location on Mother's Home Range <sup>a</sup>	Maximum Trapping Interval (Days) <sup>b</sup>
<b>Radio-tagged Juveniles</b>		
Males	43.5 (15)	----
Females	58.2 (17)	----
<b>All Ear-tagged Juveniles</b>		
Males	42.4 (25)	6.4 (11)
Females	44.4 (28)	29.0 (15)
<b>All Untagged Juveniles*</b>		
Males	----	9.5 (62)
Females	----	22.8 (57)

<sup>a</sup> Mean age at last location in mother's home range calculated for all juvenile hares tagged as newborns and either 1) still radio-tagged at 28 days of age, or 2) caught in a live-trap at any age.

<sup>b</sup> Maximum trapping interval = number of days between first and last capture in live-traps for 1) all juveniles eartagged as newborns, or 2) all untagged juveniles first captured weighing less than 500 g.

\* Significant difference between males and females (Mann-Whitney U-test,  $0.02 < P < 0.05$ ).

after 28 days of age. Secondly, I calculated the same index for all juvenile hares tagged as newborns and subsequently retrapped in live-traps at any age. Finally, I calculated the number of days between the first and last capture in a live-trap of 1) all juveniles tagged as newborns, and 2) all juveniles first captured weighing less than 500 g. All of these indices suggest that female juveniles remained on their natal ranges for longer than males, although the difference was statistically significant only between the trapping-interval indices for untagged males and females (Table 3.1).

Few of the juvenile hares born in my cages in 1989 settled down on the study grids to breed in 1990, so I have few data on breeding dispersal distances. Of the 86 tagged juveniles estimated to have survived to weaning age in 1989 (296 total juveniles X 0.29 survival rate to weaning), only four bred the next year on the grids where they were born. All four were females, one born in the first litter, two in the second litter, and one in the third litter of 1989. Of the 119 untagged juvenile hares first captured at less than 500 g, ten were breeders on the same grids in 1990. These animals were of unknown origin, but at weaning age, few animals weighed more than 500 g (Chapter 1), so it is likely that they were born on or near the grids. Four of these were first litter males, and six were females (one from first litter, and five from second litter). I found no difference between the survival rates of radio-tagged male and female juvenile hares (Chapter 2). Therefore, these data suggest that females may not disperse as far as males, and that first litter males have a higher probability than later litter males of establishing home ranges near their natal ranges.

## *DISCUSSION*

These data are the first collected on pre-dispersal movements of juvenile snowshoe hares in the wild using a large sample size. They are largely consistent with the pattern suggested by previous studies on captive hares and one wild litter (Severaid 1942; Rongstad & Tester 1971; Graf & Sinclair 1987). Juvenile hares leave their natal "nests" at an early age, as do European hare (*Lepus europaeus*) leverets (Broekhuizen & Maaskamp 1980; Martinet & Demarne 1984). The dispersion of littermates in separate hiding places after litter break-up was also found for European hares (Broekhuizen & Maaskamp 1980), but it is contrary to the observation of Graf & Sinclair (1987) that juvenile hares often rested in groups of 1-6. Their results were perhaps the consequence of limited movements of penned hares. My data showing the occasional mixing of hare litters are consistent with those of Graf & Sinclair (1987) for snowshoe hares, and Broekhuizen & Maaskamp (1980) and Martinet & Demarne (1984) for European hares. Sorenson, Rogers & Baskett (1972) experimentally switched swamp rabbit (*Sylvilagus aquaticus*) juveniles between nests and found that strange young were readily accepted. Many female lagomorphs may therefore show little recognition of their offspring.

The movements of juvenile snowshoe hares increased rapidly to the age of 20 days, and stayed about the same for the next two weeks. I did not have good measures of the sizes of adult female home ranges, so I was unable to relate the juvenile home ranges to those of their mothers. In the snowshoe hare population peak of 1980-81, Boutin (1984b) found that the mean radius

of adult home ranges was about 90 m. If the home ranges of adult females were of similar size in this study, then the sizes of the juvenile home ranges were about 70% of those of their mothers from 20-35 days of age, assuming that the juvenile nest sites were at the approximate geometric centres of their natal ranges. Juvenile movements again increased after 35 days of age, which may have been related to exploratory behaviour before dispersal, or to increased aggression from their mothers, most of which had newborn litters after 35 days.

The few data which C. Bergman and I collected on maternal-juvenile relations are also consistent with those reported in the literature. A short, single nursing period, closely related to the time of twilight, has been noted for snowshoe hares (Rongstad & Tester 1971; Graf & Sinclair 1987), European hares (Broekhuizen & Maaskamp 1980), and swamp rabbits (Sorenson, Rogers & Baskett 1972). Sorenson, Rogers & Baskett (1972) found that adult female swamp rabbits often responded to juvenile distress cries, as also reported for snowshoe hares (Graf & Sinclair 1987). Graf & Sinclair also observed a mother try, but fail, to protect her offspring from predation by a grey jay (*Perisoreus canadensis*). My observations of female hares chasing red squirrels and ground squirrels from their litters suggest that females may also be successful in defending their young from small predators (see Chapter 2). The extended nursing period that I observed for third litter juveniles has also been noted in European hares (Broekhuizen & Maaskamp 1980), and is likely valuable in supplementing juvenile nutrition

during the late summer and early autumn when most herbaceous food plants were senescent.

The behaviour of nursing female hares and their offspring before weaning is well-adapted to minimizing predation risk, which is the largest cause of early juvenile mortality (Chapter 2). Hares have highly-concentrated milk (Martinet & Demarne 1984), which allows them to nurse for short, infrequent periods, thus minimizing the amount of time the whole litter is in one spot. The individual and widely-dispersed hiding places of juvenile littermates also minimize the chance that all would be discovered at the same time by a predator. These behavioral traits may be characteristic of leporids.

I was able to determine dispersal distances from natal to breeding ranges for few animals, so I have little information on absolute distances of natal dispersal, or zygote-to-zygote distances (Shields 1987). The pattern of sudden disappearance of many animals from their natal ranges between the ages of 30 and 45 days suggests that much dispersal may involve long-range (> 1 km) movements in less than one day. Of the four radioed dispersers which I was able to relocate, three had travelled over 700 m, and the other 250 m, from their locations on the previous day. The suggestion that females may settle closer to their natal ranges is based on few data, but nonetheless, none of the males born in my cages were known to have settled on the grids where they were born, while four females did so.

My data indicate that many juvenile hares disperse soon after weaning, confirming Boutin's (1984a) suggestion that much mixing of

populations through juvenile dispersal occurs during the summer. High rates of juvenile dispersal were noted at peak hare numbers by Windberg & Keith (1976) in Alberta, and by Boutin *et al.* (1985) in the Yukon. As food and space may both be in short supply at peak hare numbers (Keith & Windberg 1978; Boutin 1984a), juvenile dispersal at this time may be characterized as saturation dispersal (Lidicker 1975). Dispersal at this time is predicted to be mostly by social subordinates such as juveniles, which have relatively low chances of surviving to breeding (Lidicker 1975). The proximate causes stimulating juvenile dispersal are poorly understood (see Lidicker 1975; Bekoff 1977; Gaines & McClenaghan 1980).

Mammalian natal dispersal is predominantly biased towards males (Greenwood 1980), and this pattern holds for most small mammals with multi-annual population cycles (Krebs *et al.* 1976; Gaines & McClenaghan 1980; Boonstra *et al.* 1987; but see Myers & Krebs 1971). However, neither Windberg & Keith (1976) nor Boutin *et al.* (1985) found a biased sex ratio among snowshoe hares dispersing to removal and control grids. My data suggest that, at least at peak hare numbers, juvenile males may disperse earlier and farther than females.

The potential advantages of earlier dispersal of male juvenile hares are unclear. Boutin (1984a) found lower rates of immigration into a control population in the autumn than in the summer. He suggested that adult hares may be more tolerant of juveniles moving into their home ranges during the summer than in the fall or winter, as very few juveniles are breeders, and competition for food is likely less in the summer than later in

the year. Graf (1985) found that adult males were more aggressive than females, and that adults may act aggressively towards potential juvenile immigrants (also see Boutin 1984a). Windberg & Keith (1976) removed males from one grid, and females from another, to examine the effects of imbalanced sex ratios on subsequent immigration. They found that adult emigration from the grids in summer, and juvenile ingress in the fall and winter acted to balance the sex ratios within a year, suggesting that conspecifics may limit immigration of same-sex animals. Juvenile males may encounter higher levels of aggression than juvenile females, and earlier dispersal may increase their chances of successfully settling on a new home range. There is some evidence for this in my data. All four of the juvenile males suspected of settling on their natal grids were first litter juveniles, and thus of adult size in the autumn. In contrast, of the females known and suspected to have settled on their natal grids, two were from first litter, seven from second litter, and one from third litter, indicating that smaller-sized (and presumably more subordinate) females were able to successfully settle near their natal ranges, whereas smaller-sized males could not. This speculation is based only on circumstantial evidence, however. An analysis of dispersal by male and female juveniles of known origin to and from study areas with experimentally manipulated sex ratios is needed to clarify the role of intra-sexual competition in influencing sex-specific dispersal and immigration rates.

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## **GENERAL CONCLUSIONS**

There are several findings of interest from this study. The first is that hare reproduction, juvenile growth rates, and early juvenile survival rates were largely unchanged by the food addition. These findings are contrary to those predicted by the Keith Hypothesis (Keith 1974) that food shortage is the driving force behind the lower survival and reproductive rates observed at peak hare densities. My study indicates that reproduction and early juvenile survival were not limited by food at the peak hare densities observed in the Yukon. The possibility remains that these rates will be adversely affected by food shortage during the population decline. I do not know why my results differ from the experimental results of Windberg & Keith (1976) and Vaughan & Keith (1981) in Alberta. Both of these studies found that food addition increased reproductive, survival and growth rates relative to those of control animals. The effects of the food addition may have been confounded by the higher hare densities on my food grids (Chapter 1), and the experimental densities used in Alberta were high relative to those on all of my grids. If hare density *per se* alters the way that extrinsic factors such as food supply affect hare demography, then it is necessary to study hare populations during cycles of different amplitudes in order to determine whether a common single- or multi-factor model can explain the cycle in all populations. An experimental examination of the effects of social behaviour on hare demography would also be valuable in clarifying its role in the hare cycle (Boutin 1984; Graf 1985; Krebs 1986).

My second major finding is that early mortality of juvenile snowshoe hares is quite high, and that most losses are due to predation by small mammals (primarily red squirrels and arctic ground squirrels) (Chapter 2). The fact that animals usually thought of as herbivores are also active predators is not surprising (see Bazely 1989); however, the extent of predation by squirrels on juvenile hares was unexpected. It is not known to what degree the poor spruce cone crop on my study grids in 1989 stimulated red squirrels to search out alternative food sources, or whether the phenomenon of predation by smaller mammals on juvenile hares is widespread.

Thirdly, to my knowledge, this is the first study to find evidence of a trade-off between litter size and juvenile survival in a wild mammal, as predicted by life history theory (Stearns 1976). Smaller-sized juvenile hares were born in larger-sized litters, and they were more vulnerable to predation (Chapter 2). Female hares suffered high rates of complete litter loss, particularly in later litters of the season. Large litters of small-sized juveniles may be an adaptation to minimize the probability of complete litter loss in the face of very high predation pressure.

Finally, this study confirmed the suggestion by Boutin (1984) that many juvenile hares begin to disperse soon after weaning (Chapter 3). I also found evidence that males may disperse earlier and farther than females from their natal ranges, as is the pattern in most mammals (Greenwood 1980). The role of dispersal in the population dynamics of hares is largely unknown. However, as dispersers may have lower survival rates than

residents (e.g. Metzgar 1967), and juvenile survival is highly correlated with rates of population change in snowshoe hares (Keith & Windberg 1978; Krebs *et al.* 1986), the effects of dispersal on the demography of hares seem worth further exploration.

This study was conducted during the two peak years of hare abundance at Kluane (C. J. Krebs, unpublished data). Therefore, further studies are needed to relate reproductive output and early juvenile survival to population changes over the hare cycle. My results suggest some areas for future research that may be fruitful. Experimental manipulations of both food supply and population density would be useful in separating the effects of these factors on overall population processes. Likewise, removal experiments and sex-ratio manipulations could be used to examine the roles of spacing behaviour and dispersal in the population regulation of snowshoe hares. Although this is logistically difficult, the removal or exclusion of potential smaller predators of juvenile hares, such as squirrels, would clarify the importance of their predation on recruitment rates. Lastly, as snowshoe hares appear to be one of the few mammalian species in which the female readily accepts strange young, they are ideal subjects for testing theories of life history trade-offs through litter-size manipulations.

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