REPRODUCTION AND PRE-WEANING JUVENILE SURVIVAL
IN A CYCLIC POPULATION OF SNOWSHOE HARES

by

CAROL IRENE STEFAN

B.Sc., The University of Calgary, 1994

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES

Department of Zoology

We accept this thesis as conforming
to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

April 1998

© Carol Irene Stefan, 1998
In presenting this thesis in partial fulfilment of the requirements for an advanced
degree at the University of British Columbia, I agree that the Library shall make it
freely available for reference and study. I further agree that permission for extensive
copying of this thesis for scholarly purposes may be granted by the head of my
department or by his or her representatives. It is understood that copying or
publication of this thesis for financial gain shall not be allowed without my written
permission.

Department of Zoology

The University of British Columbia
Vancouver, Canada

Date April 29, 1998
ABSTRACT

Reproductive output and pre-weaning survival were estimated in a cyclic population of snowshoe hares (*Lepus americanus*) in the Kluane Lake region of southwest Yukon Territory. Data collected by five researchers were collated over eight years (1989 - 1996). Pregnant hares were captured and held in cages until they gave birth, so that reproductive characteristics could be measured. Newborn hares were radio-tagged to estimate survival rates from birth.

Pregnancy rate, litter size and neonate size fluctuated significantly throughout the cycle, changing about two years before corresponding changes in density. The lowest and highest values for all measured parameters were recorded during the decline and increase phases, respectively. Pregnancy rates were nearly 100% in litters born early in the breeding season, but declined up to 20% in the last litter of the year. The number of litters produced in a breeding season varied between two (decline phase) and four (low, early increase). Litter sizes varied among litters within a year, with larger litters being born later in the breeding season. Litter sizes also differed among years, ranging from a mean of 3.8 during the decline to 5.5 during the increase. The weight and size of neonates varied by 5-33% among years.

Predation was the primary cause of death of leverets in all phases of the cycle except the decline, when exposure and starvation claimed most young hares. Juvenile survival was highly variable among litter groups at peak hare densities and extremely poor during the decline, particularly Litter 2. Survival was still variable but higher during the low, and was consistently high during the increase. Red squirrels were the primary...
predators of leverets <10-d old and showed a strong functional response to increasing leveret density across years, particularly in Litter 2.

The combined changes for reproduction and early juvenile survival produced a 10-fold variation in pre-weaning recruitment of juvenile hares. The indirect effect of predators on the foraging behaviour and physiology of adult females and direct predation on very young hares were implicated as the cause of these changes. My results support the premise that both reproduction and early juvenile survival strongly influence the population growth rate of snowshoe hares.
# TABLE OF CONTENTS

ABSTRACT ......................................................................................................................... ii

LIST OF TABLES .............................................................................................................. vii

LIST OF FIGURES ............................................................................................................ viii

ACKNOWLEDGEMENTS ................................................................................................. ix

CHAPTER 1. GENERAL INTRODUCTION: INFLUENCE OF REPRODUCTION AND PRE-WEANING JUVENILE SURVIVAL ON THE SNOWSHOE HARE CYCLE ...... 1

CHAPTER 2. REPRODUCTIVE CHANGES IN A CYCLIC POPULATION OF SNOWSHOE HARES ............................................................................................................ 4

   INTRODUCTION ............................................................................................................. 4
   METHODS ....................................................................................................................... 5
      Study site .................................................................................................................... 5
      Hare trapping ........................................................................................................... 5
      Reproductive measurements and litter characteristics ............................................ 9
      Analysis .................................................................................................................... 10
   RESULTS ...................................................................................................................... 12
      Parturition dates and gestation times .................................................................... 12
      Pregnancy rates ...................................................................................................... 14
      Stillborn Rates ....................................................................................................... 16
      Litter Sizes .............................................................................................................. 16
      Reproductive Output ............................................................................................... 20
      Neonate Measurements .......................................................................................... 20
      Sex ratios ............................................................................................................... 29
   DISCUSSION ................................................................................................................. 29
      Reproduction across the cycle ............................................................................... 29
      Maternal age and reproduction ............................................................................ 32
      Neonate measurements ....................................................................................... 34
      Why does reproduction change? ........................................................................... 35
         Parasites .............................................................................................................. 36
         Food ...................................................................................................................... 36
         Predator-sensitive foraging ................................................................................. 37
         Maternal stress .................................................................................................... 38
      Conclusion ............................................................................................................. 38

CHAPTER 3. PRE-WEANING JUVENILE SURVIVAL IN A CYCLIC POPULATION OF SNOWSHOE HARES ................................................................. 40

   INTRODUCTION ............................................................................................................. 40
   METHODS ....................................................................................................................... 42
      Juvenile survival estimates .................................................................................... 42
Appendix 6. Results of log-rank comparisons for 30-day survival rates among litter groups by year .......................................................... 101

Appendix 7. Results of log-rank comparisons for 30-day survival rates among years by litter group ............................................................ 102

Appendix 8. Kaplan-Meier 30-day survival curves by litter group for all years ............ 103
LIST OF TABLES

Table 2.1. Study grids and areas used for monitoring snowshoe hare reproduction. ........ 8

Table 2.2. Mean parturition dates, gestation times and the range of parturition dates for snowshoe hares for each litter group in each year. ............................................. 13

Table 2.3. Pregnancy rates for each litter group by year............................................ 15

Table 2.4. Stillborn rates for each litter group by year. ............................................. 17

Table 2.5. Sex ratios of snowshoe hare litters............................................................ 28

Table 2.6. Comparison of reproductive parameters between snowshoe hare populations in the Yukon and Alberta................................................................. 30

Table 3.1. 30-day survival estimates for juvenile snowshoe hares by litter group for each year............................................................................................................. 50

Table 3.2. Forward step-wise logistic regression results for the influence of neonate birth weight and litter size on pre-weaning juvenile survival of snowshoe hares........... 57

Table 3.3. Proximate causes of mortality of juvenile snowshoe hares prior to weaning for all years....................................................................................................... 59

Table 3.4. Known and suspected predators of juvenile snowshoe hares prior to weaning for all years combined................................................................. 60
LIST OF FIGURES

Figure 2.1. Map of study area in the Kluane region, Yukon Territory........................................6

Figure 2.2. Mean litter sizes of snowshoe hares........................................................................18

Figure 2.3. Reproductive output and population changes for snowshoe hares for the same phases of the cycle in the Yukon and Alberta.............................................................21

Figure 2.4. Mean birth weight and mean right hind foot length of newborn snowshoe hares ............................................................................................................................23

Figure 2.5. Mean residuals of birth weight for newborn snowshoe hares..................................26

Figure 3.1. Inter-grid comparison of 30-day juvenile snowshoe hare survival for Controls 1, 3, 4 and off grid for 1994 through 1996........................................................................48

Figure 3.2. Correlation results between pre-weaning juvenile hare survival and population growth rate, adult hare survival, reproductive output and hare density in the previous year..................................................................................................................52

Figure 3.3. Calculated Kaplan-Meier survival curves treating missing animals as either censored, all dead or all surviving to 30 days.................................................................54

Figure 3.4. Functional response of red squirrels to changes in leveret density for each of the three litter groups.................................................................................................64

Figure 3.5. Changes in number of juvenile snowshoe hares weaned per female across the snowshoe hare cycle........................................................................................................66

Figure 3.6. Correlation between mean annual recruitment rate and population growth rate ........................................................................................................................................68

Figure 3.7. 30-day juvenile survival for Control 3 only.................................................................73
ACKNOWLEDGEMENTS

This thesis and my graduate career were greatly enriched by so many incredible people, both in the field and at home, that I hardly know where to begin. First, I wish to thank my supervisor, Charles Krebs for his guidance, wisdom and good humour and for providing me with the tremendous opportunity to be part of the Kluane Project. I will be forever grateful to Mark O’Donoghue and Cathy Doyle, who were so generous with their time and knowledge, and who first introduced me to the intriguing and beautiful snowshoe hare and those amazing baby bunnies. I have worked with so many terrific people, but I especially wish to thank my burrowmates, Tim Karels and Elizabeth Gillis, and fellow bunny biologist, Karen Hodges, for sharing endless encouragement, cheer, insight, and friendship.

I received invaluable assistance in the field from Josie Hughes, Cathy Doyle, Elizabeth Gillis, Karen Hodges, Teresa Chu, Jordan deGroot, Jan Jekielek, Frank Doyle, Martin Predavec, Christie Spence, Tim Karels, Gillian Turney, Louisa Pulfrey, Fiona Danks, Helen Jewell, Johan Stroman, Scott Grindal and countless energetic volunteers. My thesis is much more comprehensive owing to the data collected and contributed by Mark O’Donoghue, Cathy Doyle, John Sovell and Bob Kull.

Thank you to Dan Haydon, who was ever tolerant of my many statistical questions, and for not only providing answers but for helping me understand them. I am truly grateful for the thoughtful suggestions and comments contributed by Karen Hodges, Dennis Chitty, Scott Grindal and the Mouse Tea discussion group. I would like to thank my committee, Tony Sinclair, Robin Liley, Don McPhail and, particularly, Jamie Smith, for providing helpful comments and challenging me with interesting questions. I am also grateful to Lance Bailey and Alistair Blachford who were always available to answer any computer related queries. My time in graduate school was also enlivened by the ‘red dot club’; my peers who were there from the beginning.

To the remarkable crew at Kluane - I have been so fortunate to have shared so many memorable days with you in the most glorious place. How lucky that the days at Kluane last so long. The Arctic Institute of America was my home for three wonderful summers and my time there was also made more enjoyable by Andy and Carole Williams and the hearty feasts prepared by Jan Williams. Jocelyn McDowell at Kluane and Irene Wingate at UBC provided technical support and brilliantly coordinated the numerous researchers and equipment.

I was financially supported by graduate research and teaching assistantships from the Department of Zoology. Research funds were provided by a Natural Science and Engineering Research Council grant to C.J. Krebs. Living expenses at Kluane were partially funded by Northern Studies Training Program grants.

I dedicate this thesis to my parents, Paul and Nellie Stefan, whose constant love and support always inspired me to reach higher while remaining firmly grounded. To my brothers and sister, Paul, Sheila, and Frank, and their wonderful families, I am so grateful for your encouragement and for always keeping me close no matter where I was.

Finally, to Scott. Thank you for always knowing when to distract me and when to help me focus, and for always making me laugh.
CHAPTER 1. GENERAL INTRODUCTION: INFLUENCE OF REPRODUCTION AND PRE-WEANING JUVENILE SURVIVAL ON THE SNOWSHOE HARE CYCLE

Recruitment is a composite of several demographic parameters including reproductive rate and pre- and post-weaning juvenile survival. Of these parameters, changes in post-weaning juvenile survival have the strongest influence on the cyclic population dynamics of snowshoe hares (Keith and Windberg 1978, Krebs et al. 1995). However the relative influence of reproductive rate and pre-weaning juvenile survival on the cyclic changes in the summer recruitment of juvenile hares is controversial.

According to Keith and Windberg (1978) and Cary and Keith (1979), the observed changes in recruitment are due solely to changes in reproduction. Others (Krebs et al. 1986, O'Donoghue 1994) believe that pre-weaning juvenile survival, in concert with changes in reproduction, greatly affects population growth rate. Previous research has clearly shown that changes in reproduction precede corresponding changes in snowshoe hare density (Cary and Keith 1979). There is some debate over the causes of these changes in reproduction. The variation in reproduction was attributed by Cary and Keith, to poor food resources at peak hare densities and the amount of over-winter weight loss in the previous winter. Others suggest that reproduction could be the affected by changes in parasite load (Sovell and Holmes 1996, Murray et al. 1997), predation-sensitive foraging (Hik 1995), or fluctuating stress levels imposed by predation risk (Boonstra et al. 1998a).

There is limited information about survival of juvenile hares prior to weaning. Although very young hares suffer high mortality in the wild (O'Donoghue 1994), it is not
yet known whether pre-weaning survival is related to the hare cycle. Estimates of juvenile hare survival from birth to 45-d were not correlated with population growth rate in a cyclic population of snowshoe hares in Alberta (Keith and Windberg 1978). The changes in the proportion of live-trapped juveniles to adults through the cycle were therefore attributed to changes in reproductive rate alone. In contrast, for another cyclic population of snowshoe hares in the Yukon (Krebs et al. 1986), the estimated changes in reproductive rate could only explain one-half of the 5.3-fold change in juvenile recruitment to the live-trapped population through the cycle. Thus, it was concluded that early mortality rates of juvenile hares must also fluctuate cyclically.

What are the factors that might contribute to differences in pre-weaning juvenile survival through the hare cycle? As seen for adult hares, changes in the numerical (Krebs et al. 1995, O'Donoghue et al. 1997) or functional (O'Donoghue 1997) responses of predators could differentially affect survival of young hares throughout the cycle. In addition, if maternal condition is compromised by cyclic variation in food abundance (Keith 1983, Krebs et al. 1995) or by the effects of chronic stress (Boonstra et al. 1998a), and maternal condition affects pre-weaning juvenile survival, we would see coincident changes.

My aim was to estimate how many juvenile hares survive to weaning across one snowshoe hare cycle. I measured reproductive parameters including litter sizes, pregnancy rates, and stillborn rates to calculate reproductive rates through the cycle. I also directly measured juvenile survival rates through radio-telemetry and compared the proximate causes of mortality among years to ascertain whether pre-weaning juvenile survival was related to the hare cycle. The cause of death will help us determine the reasons for the
change, or lack of change, in survival. Since red squirrels were the primary predator at peak hare densities (O'Donoghue 1994), I tested the functional response of this small predator to assess its potential affect on the population growth rate. By measuring the separate demographic components that contribute to early juvenile recruitment, I assessed the relative influence of reproduction and pre-weaning survival on the cyclic dynamics of snowshoe hares.
CHAPTER 2. REPRODUCTIVE CHANGES IN A CYCLIC POPULATION OF SNOWSHOE HARES

INTRODUCTION

The causes of cyclic fluctuations in density of snowshoe hare (Lepus americanus) populations have been debated vigorously (Green and Evans 1940, Trostel et al. 1987, Keith 1983, Krebs et al. 1995, Murray et al. 1997, Boonstra et al. 1998a). Some of these studies have examined reproduction and reported cyclic changes in reproductive parameters related to the population growth rate. In a 16-year study of a snowshoe hare population in Alberta, Cary and Keith (1979) used necropsy studies to determine litter sizes, and ovulation and pregnancy rates. From these findings, they calculated that the number of young produced per female varied 2.4-fold during a cycle. Changes in reproduction preceded corresponding changes in density by about three years. In another long-term study, Krebs et al. (1986) live-trapped snowshoe hare populations in the Yukon. They did not measure reproductive parameters directly; however, they observed variation in the length of the breeding season and a strong correlation between juvenile recruitment and the rate of population change. Although these two studies disagreed about the role of over-winter food resources in causing the changes in hare density, the similarities in the patterns of reproductive change and juvenile recruitment warrant further investigation.

The objective of this study was to describe reproductive changes spanning eight years of the snowshoe hare cycle, in the Kluane region of the Yukon. I predicted that this population would show variation in reproductive parameters across the cycle similar to
those found by Cary and Keith (1979) in Alberta. I collected data during increasing hare densities in 1995 and 1996, and compared these with data collected by other researchers in previous years at the same sites. This study was unique because we measured reproduction by following individual hares through pregnancy in a capture-release technique that also permitted us to count and measure live young.

METHODS

Study site

The study area was located in the Shakwak Trench east of Kluane Lake, Yukon Territory (61° N, 138° W). This boreal forest region is dominated by white spruce (Picea glauca) mixed with a patchy understory of shrubs, primarily grey willow (Salix glauca), bog birch (Betula glandulosa) and soapberry (Sheperdia canadensis), and herbaceous plants. For a more detailed description of the area, see Douglas (1974).

Hare trapping

Snowshoe hare populations were monitored via live-trapping sessions conducted throughout the breeding season (April-August) from 1989 to 1996, with the exception of 1993. In 1993, reproduction was not measured, but live-trapping was conducted in the spring and fall to obtain density estimates. In all years, trapping occurred on existing 36-ha control grids established as part of the Kluane Boreal Forest Ecosystem Project (Figure 2.1). There were 86 Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin) on each grid, placed 30 m apart along four evenly spaced rows. Table 2.1
Figure 2.1. Map of study area in the Kluane region, Yukon Territory. Control grids and off grid areas where reproduction was monitored are marked. Locations of maternity areas where pregnant females were kept are also indicated.
Table 2.1. Study grids and areas used for monitoring snowshoe hare reproduction. Grid names and numbers correspond to the control grids established by the Kluane Boreal Forest Ecosystem Project.

<table>
<thead>
<tr>
<th>Year</th>
<th>Grids</th>
<th>Areas</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989</td>
<td>Control 1, Control 3</td>
<td>Sulphur, Chitty</td>
</tr>
<tr>
<td>1990</td>
<td>Control 2, Control 3</td>
<td>Silver, Chitty</td>
</tr>
<tr>
<td>1991</td>
<td>Control 2</td>
<td>Silver</td>
</tr>
<tr>
<td>1992</td>
<td>Control 1, Control 2, Control 4, off grid</td>
<td>Sulphur, Silver, Lloyd, off grid</td>
</tr>
<tr>
<td>1994</td>
<td>Control 1, Control 3, Control 4, off grid</td>
<td>Sulphur, Chitty, Lloyd, off grid</td>
</tr>
<tr>
<td>1995</td>
<td>Control 1, Control 3, off grid</td>
<td>Sulphur, Chitty, off grid</td>
</tr>
<tr>
<td>1996</td>
<td>Control 1, Control 3, Control 4</td>
<td>Sulphur, Chitty, Lloyd</td>
</tr>
</tbody>
</table>
outlines which grids were used in which year. In 1992, 1994, and 1995, when hare densities were low, I also set single rows of traps in off-grid areas (Figure 2.1).

Captured hares were held in burlap bags while being handled in order to reduce stress. I weighed each hare, measured the right hind foot as an index of body size (Bailey 1968), ear-tagged new animals (No. 3 monel tags, National Band and Tag Co., Newport, Kentucky, USA), and determined the reproductive status for both sexes (O'Donoghue and Krebs 1992).

**Reproductive measurements and litter characteristics**

The protocol for handling and care of adult female and newborn hares has remained consistent for all the studies of reproduction conducted in conjunction with the Kluane Project, beginning in 1989 (ODonoghue and Krebs 1992).

Snowshoe hares have multiple litters each summer, and mating occurs immediately post-partum. Breeding starts in early spring and parturition remains synchronous over the breeding season (Cary and Keith 1979, O'Donoghue and Boutin 1995), which results in distinct litter groups. Trapping for pregnant females focused around these peak times. We determined the stage of a hare’s pregnancy by her weight, the colour of the lactational tissue, and by gently palpating her abdomen. Hares estimated to be in the last week of pregnancy were placed in individual 60×60×120cm chicken wire cages (O'Donoghue and Krebs 1992). To minimize disturbance by predators and researchers, cages were located within electrically fenced enclosures at least 200m away from the grids. The cages provided shelter, a partitioned (spruce branch or burlap sheet) area of refuge, and straw for nesting
material. Until they gave birth, the mother hares were checked, watered, and fed rabbit chow, apples, and natural forage each morning. The morning after the hares gave birth, I removed the females from the cage and counted the young. I sexed, weighed, eartagged (No. 1 monel tags), and measured the right hind foot length of each newborn hare.

The mother hare and her litter were then immediately returned to the female’s home range, near to where she was trapped. I placed the young hares in a nest that I created, generally at the base of a willow, under deadfall, or at the base of a cluster of trees, such that the mother could easily find her litter. Before placing the young in the litter site, I held them up to their mother, who was held in a Tomahawk trap. Once the litter was settled and I opened the trap, the female was allowed to leave when she was ready, often stepping up to or over the litter before hopping away.

**Analysis**

I pooled the data from all areas because I considered individual hares to be the unit of measurement and any variability among control areas to represent the natural variation in the study area population as a whole.

Pregnancy rates were calculated based on the proportion of reproductive females trapped within one week of the mean parturition date for each litter group. I also used necropsy studies to obtain additional data on litter sizes and parturition dates (estimated from prenatal leveret size as per Bookhout 1964 and Dell and Schierbaum 1974). Gestation periods were estimated in two ways for Litters 2 and 3. I compared gestation periods calculated from mean parturition dates and compared these with gestation periods only from
females trapped for successive litters. Conception dates for Litter 1 were not known, so
gestation periods could not be determined for this litter.

To eliminate any dependence between the birth weight of litter mates, I used mean
birth weight and mean right hind foot length for each litter in the analyses. Only birth
weights of live young were used. Newborn hares were determined to be stillborn if the
necropsy results indicated that the lungs had not inflated (i.e., were dark in colour and sank
in water) and there was no internal trauma. Stillborn rates were determined by calculating
the proportion of stillborn young to total young born, excluding newborn hares that were
dead but the cause of death could not be confirmed.

To obtain a density estimate for hares for each year, I averaged the spring density
estimates provided by the Kluane Project [average of program CAPTURE (Otis et al. 1978)
and Jolly-Seber method (Seber 1982)] for the Control grids 1, 2 and 3 (Krebs et al.
unpublished data) to provide an overall estimate for the entire valley.

Age of the mother was calculated from the age of each hare at first capture starting
in 1986 (Hodges et al. in prep.). All animals were eartagged at first capture and, as the
dispersal rate of adults was low (<10%; K.E. Hodges, unpublished data), any new animals
on each grid in the spring were assumed to be yearlings and assigned a minimum age of one.
We assigned “known” ages to animals caught as juveniles during the summer or fall and
added one year to each age class on January 1st. We pooled minimum age and known age
categories for each year to arrive at the age distribution across the cycle. I used these
assigned ages to group individual female hares into categories of “yearling” or “2 years old
and older”.

11
The total reproductive output per female per year was estimated by multiplying mean litter size by pregnancy rate summed for all litter groups. I did not incorporate stillborn rates when presenting reproductive output results, so that I could make direct comparisons to the "potential natality" values reported by Cary and Keith (1979). However, stillborn rates can impact actual natality as observed during the first year of the decline in 1991.

All results were reported using a significance level of p<0.05. I performed an analysis of variance (Statistica®, StatSoft 1995) to compare mean parturition date of the first litter among years and two-way analysis of variance (SuperANOVA, Gagnon et al. 1991) to compare among litter groups and among years for mean litter size and for mean birth weight. Tukey's test for unequal sample sizes (Spjotvoll and Stoline test) was used for all post-hoc comparisons of the above analyses. I used Pearson's correlation (Statistica®, StatSoft 1995) to determine the relationship between neonate birth weight and right hind foot length. Log-linear analyses (Statistica®, StatSoft 1995) were used to compare pregnancy rates, stillborn rates, and sex ratios among litter groups and years.

RESULTS

Parturition dates and gestation times

Timing of the first litter varied significantly across years (F=25.36, df=57, p<0.001), but occurred in the third week of May in four of the seven years examined (Table 2.2). The mean birth date occurred about one week later than average in 1991 and 1992, and nearly two weeks earlier in 1994. The reported mean gestation time for snowshoe hares is 36-40 days (mean: 37.2 days; Severaid 1942). The shorter gestation times observed in this study,
Table 2.2. Mean parturition dates, gestation times and the range of parturition dates for snowshoe hares for each litter group in each year. Sample sizes were based on the number of pregnant hares that were caged and subsequently gave birth. Gestation periods were calculated from the difference between mean parturition dates and repeat females separately.

<table>
<thead>
<tr>
<th>Year</th>
<th>Litter Group</th>
<th>Mean Parturition Date</th>
<th>SE (days)</th>
<th>Mean Gestation Period (days)</th>
<th>n</th>
<th>Gestation Period based on individuals‡</th>
<th>n‡</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989</td>
<td>1</td>
<td>25 May</td>
<td>0.7</td>
<td>8</td>
<td></td>
<td></td>
<td>1</td>
<td>23 May - 29 May</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>2 July</td>
<td>0.9</td>
<td>13</td>
<td>1</td>
<td></td>
<td></td>
<td>26 June - 7 July</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>7 August</td>
<td>1.3</td>
<td>7</td>
<td>2</td>
<td></td>
<td></td>
<td>2 August - 13 August</td>
</tr>
<tr>
<td>1990</td>
<td>1</td>
<td>24 May</td>
<td>0.6</td>
<td>14</td>
<td></td>
<td></td>
<td></td>
<td>20 May - 29 May</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>26 June</td>
<td>0.7</td>
<td>27</td>
<td>5</td>
<td></td>
<td></td>
<td>21 June - 5 July</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>31 July</td>
<td>0.4</td>
<td>19</td>
<td>8</td>
<td></td>
<td></td>
<td>28 July - 5 August</td>
</tr>
<tr>
<td>1991</td>
<td>1</td>
<td>29 May*</td>
<td>1.1</td>
<td>7</td>
<td></td>
<td></td>
<td>3</td>
<td>27 May - 3 June</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>6 July</td>
<td>0.7</td>
<td>11</td>
<td>3</td>
<td></td>
<td></td>
<td>2 July - 9 July</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>-</td>
<td>-</td>
<td>0</td>
<td>-</td>
<td></td>
<td></td>
<td>-</td>
</tr>
<tr>
<td>1992</td>
<td>1</td>
<td>31 May**</td>
<td>3.0</td>
<td>6</td>
<td></td>
<td></td>
<td>0</td>
<td>29 May - 11 June</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>6 July</td>
<td>4.5</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td>26 June - 11 July</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>-</td>
<td>-</td>
<td>0</td>
<td>-</td>
<td></td>
<td></td>
<td>-</td>
</tr>
<tr>
<td>1994</td>
<td>1</td>
<td>12 May †</td>
<td>0.8</td>
<td>11</td>
<td></td>
<td></td>
<td>7</td>
<td>9 May - 17 May</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>18 June</td>
<td>1.0</td>
<td>9</td>
<td>2</td>
<td></td>
<td></td>
<td>14 June - 24 June</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>25 July</td>
<td>1.2</td>
<td>10</td>
<td>7</td>
<td></td>
<td></td>
<td>20 July - 2 August</td>
</tr>
<tr>
<td>1995</td>
<td>1</td>
<td>22 May</td>
<td>2.4</td>
<td>6</td>
<td></td>
<td></td>
<td>7</td>
<td>16 May - 2 June</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>20 June</td>
<td>1.3</td>
<td>9</td>
<td>2</td>
<td></td>
<td></td>
<td>13 June - 27 June</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>28 July</td>
<td>1.4</td>
<td>8</td>
<td>7</td>
<td></td>
<td></td>
<td>28 July - 2 August</td>
</tr>
<tr>
<td>1996</td>
<td>1</td>
<td>22 May</td>
<td>0.7</td>
<td>12</td>
<td></td>
<td></td>
<td>10</td>
<td>19 May - 28 May</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>27 June</td>
<td>0.9</td>
<td>14</td>
<td>2</td>
<td></td>
<td></td>
<td>22 June - 4 July</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>2 August</td>
<td>0.6</td>
<td>13</td>
<td>10</td>
<td></td>
<td></td>
<td>30 July - 5 August</td>
</tr>
</tbody>
</table>

* significantly later than 1994-1996; p<0.05
** significantly later than 1990, 1994-1996; p<0.05
† significantly earlier than all other years; p<0.001
particularly for the second litter in 1990 (33 days) and 1995 (28.8 days), were likely the result of catching females that were not trapped for the first litter but caught earlier than average for the next litter. For individual females that were caught more than once in a breeding season, mean gestation times (36-38.5 days) fell within the expected range.

**Pregnancy rates**

Two litters were produced in 1991 and 1992, three litters in 1989, 1990, and 1996, and four litters in 1994 and 1995. Previous papers (Krebs et al. 1995, Boonstra et al. 1998a) from the Kluane Project reported only one litter in 1992; however, data from two caged females as well as necropsy results for that year indicated that there was also a second litter. Although we trapped pregnant hares in the fourth litter in 1994 and 1995, pregnancy rates and litter characteristics were not measured. Pregnancy rates differed significantly among years ($\chi^2=57.38$, df=6, $p<0.001$) and litter groups ($\chi^2=25.23$, df=2, $p<0.001$). All females trapped in 1994 through 1996 were pregnant (Table 2.3). In other years, almost all females were pregnant for each litter period (77%-100%), but the rate varied by litter group, with the lowest pregnancy rates (<87%) occurring in the last litter of the year, except in 1992. In 1991 and 1992, none of the females we trapped were pregnant with a third litter.
Table 2.3. Pregnancy rates (as %) for each litter group by year. Percentages were calculated from the percentage of reproductive females of all females trapped (n) within one week of the mean parturition date for each litter group. Pregnancy rates for the fourth litter in 1994 and 1995 were not measured. *As trapping records were not available for the 2nd litter in 1992, the sample size used for this analysis was an estimate of number of female hares based on previous trapping success in 1992 and factoring in adult mortality.

<table>
<thead>
<tr>
<th>Year</th>
<th>Litter 1</th>
<th>Litter 2</th>
<th>Litter 3</th>
<th>Litter 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989</td>
<td>90.9 (32)</td>
<td>96.8 (31)</td>
<td>82.4 (34)</td>
<td>-</td>
</tr>
<tr>
<td>1990</td>
<td>89.4 (67)</td>
<td>96.2 (52)</td>
<td>86.4 (50)</td>
<td>-</td>
</tr>
<tr>
<td>1991</td>
<td>100 (7)</td>
<td>85 (13)</td>
<td>0 (13)</td>
<td>-</td>
</tr>
<tr>
<td>1992</td>
<td>77 (9)</td>
<td>100 (9)</td>
<td>0 (7*)</td>
<td>-</td>
</tr>
<tr>
<td>1994</td>
<td>100 (14)</td>
<td>100 (8)</td>
<td>100 (8)</td>
<td>n/a</td>
</tr>
<tr>
<td>1995</td>
<td>100 (17)</td>
<td>100 (17)</td>
<td>100 (12)</td>
<td>n/a</td>
</tr>
<tr>
<td>1996</td>
<td>100 (29)</td>
<td>100 (21)</td>
<td>100 (27)</td>
<td>-</td>
</tr>
</tbody>
</table>
**Stillborn Rates**

Few young were stillborn in most years and litter groups, with only two values >10% (Table 2.4). Stillborn rates varied among years ($\chi^2=24.72$, df=6, $p<0.001$) but not strongly by litter groups ($\chi^2=4.10$, df=2, $p=0.13$). Few or no stillbirths occurred in Litter 1 (0% in 5 of 7 years) but the stillborn rate increased to an average of ~7% in both later litter groups. By far, the highest stillborn rate (30.4%) occurred in the second litter of 1991, the first year of the decline. The very low stillborn rates for Litter 1 were similar to those reported for an island population of snowshoe hares located within 60 km of our study site (0% over two years, Jardine 1995). However in contrast to the increasing stillborn rates on the mainland, stillborn rates continued to be low (1%) in later litter groups on the island.

**Litter Sizes**

There was no effect of age of the mother on litter size ($F=0.34$, df=1, $p=0.56$), so the age classes were pooled. There was significant variation in mean litter size among years (3.8-5.5; $F=2.78$, df=6, $p<0.02$), among litter groups (3.6-5.8; $F=39.59$, df=2, $p<0.001$), and a significant interaction between year and litter group ($F=3.48$, df=10, $p<0.001$; Figure 2.2). Litter sizes during the early decline, in 1991, were significantly smaller (3.8) than during the increase in 1995 (5.5) and 1996 (5.3). Litter sizes for Litters 2 and 3 were not different from each other (5.8 and 5.3, respectively) but were significantly larger than Litter 1 (3.6).
Table 2.4. Stillborn rates (% stillborn, total n) for each litter group by year. Stillborn rates were calculated from the percentage of hares confirmed to be stillborn based on necropsy studies of dead newborn hares.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Litter 1</td>
<td>0 (29)</td>
<td>7.3 (55)</td>
<td>0 (20)</td>
<td>0 (13)</td>
<td>3.1 (32)</td>
<td>0 (17)</td>
<td>0 (40)</td>
</tr>
<tr>
<td>Litter 2</td>
<td>7.7 (78)</td>
<td>4.5 (156)</td>
<td>30.4 (46)</td>
<td>0 (6)</td>
<td>0 (48)</td>
<td>1.6 (62)</td>
<td>6.3 (80)</td>
</tr>
<tr>
<td>Litter 3</td>
<td>6.3 (32)</td>
<td>13.6 (81)</td>
<td>-</td>
<td>-</td>
<td>4.7 (64)</td>
<td>8.9 (45)</td>
<td>1.3 (79)</td>
</tr>
</tbody>
</table>
Figure 2.2. Mean litter sizes of snowshoe hares for Litters 1 (●), 2 (◇) and 3(■) for all years. Population changes indicated by density estimates (—).
Reproductive Output

Total reproductive output varied by year (Figure 2.3a), plunging sharply from 12.8 young per female at peak hare densities in 1990 to low of 6.9 (1991) and 7.0 (1992) during the decline. By 1994, and also in 1995, snowshoe hares were producing an estimated maximum of 18.9 young per female. For these two years, where the fourth litter was not measured, I estimated the total reproductive output by adding three young per female to the reproductive output from the first three litters. This addition represented a mean litter size of four $\times$ 85% pregnancy rate, conservative estimates based on last litter values from other years. Although litter sizes remained larger than average in 1996, the absence of a fourth litter caused a drop in reproductive output to 15.5 young per female early in the increase phase of the cycle.

Neonate Measurements

I analysed birth weight and right hind foot length of newborns, separately, and found similar but not identical patterns. Mean birth weight varied significantly with year ($F=9.67, df=6, p<0.001$), litter group ($F=21.16, df=2, p<0.001$), and age of the mother ($F=8.79, df=1, p<0.005$), but there was no interaction of year and litter group ($F=1.62, df=10, p=0.10$; Figure 2.4a). Newborns in 1990 (peak), 1995 and 1996 (increase) were 10-20g heavier than in 1991 (decline) and birth weights increased from the decline through the increase phase. Mean birth weights from Litters 1 and 2 did not differ from each other but were 5-20g lighter than birth weights from Litter 3. Yearling females had slightly smaller young (61.8g ± 0.98 SE) than older females (66.1g ± 2.72 SE). This trend appeared in four of the six years where both age classes were represented (Appendix 1).
Figure 2.3. Reproductive output (●) and population changes (—) for snowshoe hares for the same phases of the cycle in the Yukon (a) and Alberta (b). The peak phases are vertically aligned between locations (Yukon, 1990; Alberta, 1971) for ease of interpretation. Litter 4 pregnancy rates (85%) and litter sizes (4) for 1994 and 1995 in the Yukon were estimated based on last litter values from other years and added to the total for the first three litters (O). Measurements of reproduction were not taken for 1993 in the Yukon. Alberta data was modified from Cary and Keith (1979). The trends between the two regions are similar, except that reproductive output in the Yukon reached a maximum in two, rather than three, years.
Figure 2.4. Mean birth weight (a) and mean right hind foot length (b) of newborn snowshoe hares for Litters 1 (●), 2 (▼) and 3 (■) for all years. Population changes indicated by density estimates (—).
The age of the mother had no effect on offspring skeletal size as measured by right hind foot length ($F=1.39$, $df=1$, $p=0.24$) so the age classes of the mothers were pooled. Mean right hind foot length varied significantly with year ($F=6.89$, $df=6$, $p<0.001$) and litter group ($F=16.68$, $df=2$, $p<0.001$), but there was no interaction of year and litter group ($F=1.33$, $df=10$, $p=0.21$; Figure 2.4b). Young hares born in 1991 (early decline) were smaller than in any other year except 1992 and those born in 1996 (increase) were larger than those born during the peak (1989 and 1990) and early decline (1991). Mean right hind foot length did not differ between Litters 1 and 2, but hares born in these two litters were smaller than those born in Litter 3.

There was a significant positive relationship between right hind foot length and birth weight for newborn hares ($r^2=0.73$, $p<0.05$; Appendix 2). However, when I used right hind foot length as a covariate in an analysis of covariance comparing mean birth weights, the slopes of the regression lines were significantly different among litter groups and among years (Appendix 3). This result suggested that some groups were heavier or lighter for a given right hind foot size. To determine in which years and litter groups these differences occurred, I compared the residuals of birth weight from the regression in a two-way analysis of variance. Residuals of birth weight varied significantly across years ($F=5.91$, $df=6$, $p<0.001$), among litter groups ($F=4.74$, $df=2$, $p<0.01$), and in the interaction between year and litter group ($F=3.01$, $df=10$, $p<0.002$; Figure 2.5). Hares born during 1990 (peak) and 1996 (increase) were heavier than average for a given right hind foot length. Hares born in all other years were lighter than average, with the lightest hares born during 1992 (late decline), and were heavier through the increase. In five of the seven years, the birth weight of neonates relative to their skeletal size was essentially consistent among litter groups.
Figure 2.5. Mean residuals of birth weight for newborn snowshoe hares for Litters 1 (●), 2 (◇) and 3(■) for all years. Population changes indicated by density estimates (—).
Table 2.5. Sex ratios of snowshoe hare litters (proportion of females; number of neonates). Sex ratios did not differ significantly from 50:50.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Litter 1</td>
<td>0.42 (19)</td>
<td>0.53 (47)</td>
<td>0.69 (16)</td>
<td>0.5 (12)</td>
<td>0.42 (33)</td>
<td>0.56 (18)</td>
<td>0.51 (41)</td>
</tr>
<tr>
<td>Litter 2</td>
<td>0.54 (72)</td>
<td>0.57 (144)</td>
<td>0.63 (46)</td>
<td>0.5 (6)</td>
<td>0.44 (52)</td>
<td>0.52 (62)</td>
<td>0.44 (81)</td>
</tr>
<tr>
<td>Litter 3</td>
<td>0.53 (30)</td>
<td>0.46 (70)</td>
<td>-</td>
<td>-</td>
<td>0.38 (64)</td>
<td>0.49 (45)</td>
<td>0.51 (79)</td>
</tr>
</tbody>
</table>
However, condition of neonates was disparate among litter groups for 1989 and 1991, where birth weight increased throughout the breeding season. This trend was not consistent for the litter groups in the five other years.

**Sex ratios**

Sex ratios did not differ significantly from 50:50 for any litter group ($\chi^2=2.69$, df=2, p=0.26) or year ($\chi^2=11.40$, df=6, p=0.08; Table 2.5).

**DISCUSSION**

**Reproduction across the cycle**

All measured parameters of reproduction varied across the cycle and fluctuated essentially in concert. Pregnancy rates, litter sizes, and reproductive output were all lowest during the decline and highest in the late low and early increase. These trends are similar to those reported by Cary and Keith (1979). Table 2.6 compares the two studies for six parameters. The difference in the number of litter groups per breeding season and litter size was consistent with other studies comparing areas of different latitudes. In a review of reproductive parameters over the geographic range of the snowshoe hare, Keith et al. (1966) noted more litters per year, on average, at central latitudes (Alberta) and increasing litter size, almost 2 young per litter more, from south to north (Wisconsin to Alaska). Many of the studies used in Keith et al’s synopsis spanned only one to three years and, as the number of litters and litter size varies with the cycle (Table 2.3, Figure 2.2), the extent of latitudinal differences would be more clear if the phase of the cycle is known.
Table 2.6. Comparison of reproductive parameters between snowshoe hare populations in the Yukon (this study) and Alberta (Cary and Keith 1979).

<table>
<thead>
<tr>
<th></th>
<th>Yukon</th>
<th>Alberta</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Cycle length</strong></td>
<td>8 years</td>
<td>10 years</td>
</tr>
<tr>
<td><strong>Number of litters</strong></td>
<td>2-4; usually 3</td>
<td>3-4; usually 4</td>
</tr>
<tr>
<td><strong>Pregnancy rates</strong></td>
<td>lowest - decline</td>
<td>lowest - decline</td>
</tr>
<tr>
<td></td>
<td>highest - late low/early increase</td>
<td>highest - late low/early increase</td>
</tr>
<tr>
<td></td>
<td>lower rates for last litter of year;</td>
<td>lower rates for last litter of year</td>
</tr>
<tr>
<td></td>
<td>(except 1992)</td>
<td></td>
</tr>
<tr>
<td><strong>Litter sizes</strong></td>
<td>varied by year and litter group</td>
<td>varied by year and litter group</td>
</tr>
<tr>
<td></td>
<td>smallest - decline</td>
<td>smallest - decline</td>
</tr>
<tr>
<td></td>
<td>largest - late low/early increase</td>
<td>largest - late low/early increase</td>
</tr>
<tr>
<td></td>
<td>litter group 1&lt;3&lt;2 (most years;</td>
<td>litter group 1&lt;4&lt;3&lt;2 (most years)</td>
</tr>
<tr>
<td></td>
<td>litter 4 unknown)</td>
<td></td>
</tr>
<tr>
<td><strong>Mean litter sizes</strong></td>
<td>1989-1996</td>
<td>1967-1976 (one cycle)</td>
</tr>
<tr>
<td>(+SE)</td>
<td>Litter 1: 3.5 ±0.12</td>
<td>Litter 1: 2.6 ±0.20 †(2.8 ±0.22)</td>
</tr>
<tr>
<td></td>
<td>Litter 2: 5.7 ±0.16</td>
<td>Litter 2: 4.9 ±0.35 †(4.8 ±0.36)</td>
</tr>
<tr>
<td></td>
<td>Litter 3: 5.3 ±0.22</td>
<td>Litter 3: 4.7 ±0.32 †(4.6 ±0.33)</td>
</tr>
<tr>
<td></td>
<td>Litter 4: ?</td>
<td>Litter 4: 4.2 ±0.61 †(4.3 ±0.71)</td>
</tr>
<tr>
<td></td>
<td>† values for low density years</td>
<td>† values for low density years</td>
</tr>
<tr>
<td></td>
<td>- no values for 1993 (1st year of the low)</td>
<td>(1975, 1976) not included</td>
</tr>
<tr>
<td><strong>Reproductive Output</strong></td>
<td>lowest - decline</td>
<td>lowest - decline</td>
</tr>
<tr>
<td></td>
<td>highest - late low/early increase</td>
<td>highest - late low/early increase</td>
</tr>
</tbody>
</table>

30
From the information known at the time, Keith et al. (1966) suggested that two or more years of data were sufficient to control for the "sporadic" changes in litter size. However, subsequent evidence (this study, Cary and Keith 1979) indicates that variation in litter size is quite predictable across the cycle, and it is obviously necessary to know the phase of the cycle from which the data were obtained. The trend toward larger litter sizes with increasing latitude has also been described for other animals (e.g., moose, Sand et al. 1995; non-hibernating rodents and lagomorphs, Lord 1960; cottontail rabbits, Barkalow 1962).

Despite these differences, the changes in reproductive output across the cycle were very similar for the Yukon (6.9-18.9) and Alberta (7.5-17.8; Figure 2.3a, b; Appendix 4). The only exception was that fecundity remained high during the peak in the Yukon, whereas, in Alberta, it had already decreased by 32%. Since each study examined only one peak, more data are needed to determine which result is more common. The amplitude and rate of change in reproduction appears to vary with each cycle, even at the same location, and may be associated with the variation in cycle length. However, the timing of high and low reproductive output followed similar trends in both the Yukon and Alberta, with lowest values in the decline and highest values early in the increase. Similar changes in reproductive output (described by the proportion of juveniles to females) have also been reported for mountain hares (Lepus timidus) in northeast Scotland over a 14-year period (Hewson 1976).

The change in reproductive output in this study was due primarily to changes in pregnancy rates and litter sizes in later litters, as in Alberta (Cary and Keith 1979). Both studies described first a decrease in pregnancy rates and litter sizes of these later litters, followed by the loss of entire litter groups. From 1949 to 1956, in a different area of
northern Alberta, Rowan and Keith (1956) also reported decreasing pregnancy rates and litter sizes from the peak through the decline. Decreasing reproductive output later in the breeding season has often been attributed to additive costs of reproduction and diminishing body resources (Iason 1990, Reznick 1985, Clutton-Brock et al. 1983). The loss of entire litter groups in some years suggests (Cary and Keith 1979) that the condition of the hares fluctuates with the cycle. Studies of reproduction in other small mammal populations have also reported similar fluctuations in litter sizes with population trends. In Columbian ground squirrels (Spermophilus columbianus, Festa-Bianchet and King 1991) and montane voles (Microtus montanus, Pinter 1986), litter sizes were correlated with the rate of population change. In the cyclic M. montanus population, the change in litter size consistently preceded the change in density by one year, similar to the 2-3 year lag pattern observed for snowshoe hares when adjustments are made for cycle length.

Maternal age and reproduction

The age structure of the Yukon snowshoe hare population changed over the course of the cycle (Hodges et al., in prep.) such that the proportion of yearling to older females was inversely proportional to changes in reproductive output. This distribution has led some to argue that as hares age, fecundity decreases (Boonstra et al. 1998a, b). As reproductive output was a function of litter size and I found no differences in litter sizes between yearling and older females, it was not surprising that reproductive output also did not differ. The lack of difference in litter size between the age classes was supported by Cary and Keith (1979), who used an eye lens weight - age relationship from a known age distribution. In a study of mountain hares, Iason (1990) also found no difference between
yearling and older females in the number of young produced. The age distribution across the cycle was the same in the Alberta hare population (Cary and Keith 1979) and for mountain hares in Scotland (Hewson 1976).

In this study, the only significant effect of maternal age was on mean birth weight of the neonates. In some years, young born to yearling females were up to 4 g lighter on average than those born to older females. This is contrary to the senescence hypothesis (Boonstra 1994, Boonstra et al. 1998a, b). However, the differences in birth weight were potentially biased by unequal sample sizes of both age classes of mothers among years and litter groups. As birth weight varied with both factors, and the difference was less than 7%, more research is needed to determine if the observed difference is biologically meaningful.

Many of the yearling females examined could not be assigned to a litter group from the previous summer, so it was unknown whether females born later in the summer were at a disadvantage in the next year. Evidence from mountain hare populations indicated that hares born later in the summer grew more slowly and came into breeding condition later than did hares from earlier litters (Hewson 1968). Although growth rates of snowshoe hares born at the peak in the Yukon did not differ between litter groups (O'Donoghue and Krebs 1992), a trend for smaller skeletal sizes of hares during the decline (Hodges et al. in prep.) may be the result of slower growth rates, or a consequence of being smaller at birth. Growth rates of juveniles were not directly measured during the decline.

A number of studies have described either an increase in reproductive success with age (e.g., Sand 1996, Monson and DeGange 1995), or a parabolic relationship where success first increases and then decreases in later years (e.g., Weimerskirch 1992).
female snowshoe hares breed as yearlings, unlike many of the longer lived animals in the
above studies, the effect of age on reproduction, if any, may appear at the first litter, rather
than in the entire first year and may vary according to when the female was born during the
previous summer. There is some evidence of lower fertility in yearling female brown hares,
particularly early in the breeding season (Lepus europaeus, Lloyd 1968; but see Iason
1990). I did not have the power to detect small differences, as sample sizes of “known” age
animals from particular litter groups were low and variable among years.

Neonate measurements

The variation in birth weights and body size (right hind foot length) of the young
hares in this study also fluctuated with the cycle and followed a similar, but not identical,
pattern of changes to the other reproductive parameters measured. The smallest litters,
smallest body sizes, and lightest birth weights all occurred during the decline (1991 and
1992). During the increase phase (1995 and 1996), both litter size and birth weight
remained high for Litters 2 and 3, suggesting that females were in good condition
throughout the breeding season. In addition, during the late low and early increase (1994
and 1995), hares also produced a fourth litter. This was in contrast to the high density and
peak density years (1989 and 1990), where birth weights remained high for Litter 3, but
litter size decreased sharply. Preliminary analyses of changes in adult hare body condition
based on a weight-skeletal size regression suggest that the condition of adult females
changes across the cycle with condition indices decreasing from the peak through the first
year of the low (Hodges et al., in prep.).
The difficulty of trapping pregnant hares in low density populations, particularly in 1992, yielded small sample sizes, thus decreasing the power to detect statistical differences between this and other years for all parameters. Our data were not sufficient to determine whether the trend of smaller litters and smaller neonate size continues through the low phase or begins to increase already while populations are at a low.

The linear relationship of birth weight to right hind foot size for newborn hares from this study differs markedly from the curvilinear relationship seen in adult hares (Bailey 1968, O'Donoghue and Krebs 1992). Although there was some variability in birth weight for a given right hind foot length among years and litter groups, hares born in the third litter (in years when there was a third litter) were proportionately bigger than those born in the first two litters. This result suggested that adult females were still in good condition in mid-summer, most likely due to an abundance of high quality food (green shrubs and herbaceous plants) during gestation of this litter.

In general, hares born during years of peak and increasing density were larger and heavier than those born during decline years. I will discuss the consequences of size at birth on pre-weaning juvenile survival in Chapter 3.

Why does reproduction change?

Snowshoe hares are obviously capable of having four litters, even in northern latitudes, as we saw in the early increase phase. Why then, do females not always maximize their reproductive effort, particularly as they are likely to live only one or two years? Five non-exclusive hypotheses have been proposed to explain these reproductive changes:
i) parasites; ii) over-winter food shortage; iii) predation; iv) predator-sensitive foraging; and iv) maternal stress.

Parasites

Experimental reductions in parasite levels improved the condition of snowshoe hares but failed to improve reproduction during the decline (Sovell and Holmes 1996). In addition, although the offspring of untreated females died more frequently from starvation or abandonment, juvenile survival rates did not differ between the treatments. This was a one year study, and as the benefits of parasite treatments appear to increase in a second year (Murray et al. 1997), this hypothesis merits further investigation. These studies, along with two others incorporating models (Holmes 1995, Ives and Murray 1997), concluded that parasites probably could not cause the cycle, but do make hares more susceptible to malnutrition, potentially influencing reproduction and susceptibility to predation.

Food

Cary and Keith (1979) suggested that overwinter, particularly late winter, food shortages were the cause of the decline, yet reproduction began to decrease during the increase in both Alberta and the Yukon before food should have been limiting. In addition, food addition experiments conducted in the Yukon had no significant effect on reproduction at peak densities (O'Donoghue and Krebs 1992) when food resources, if they were limiting, would have been deficient.
Predator-sensitive foraging

It is clear that the lack of food by itself was not responsible for the reduced reproductive output. However, as suggested by Hik (1995) and Krebs et al. (1995), the risk of predation may have led to a “relative” food shortage contributing to a nutritional deficit. Evidence that hares choose safety over nutrition comes from movement studies which describe shifts in habitat use by snowshoe hares from open (high predation risk, high quality food) to closed habitats (reduced predation risk, low quality food; Hik 1994, Wolff 1980) during the decline. If snowshoe hares are risk-averse, the resultant poor body condition and decrease in fecundity could appear as an outcome of food shortage, discussed above. This may have been why Cary and Keith (1979) supported the food hypothesis. The main difference between food shortage and predation-sensitive foraging hypotheses lies in the timing. Both hypotheses predict high fecundity during the low phase, when food is abundant and there are few predators (Hodges 1998). However, a hare’s perception of greater predation risk would begin during the increase phase when predator numbers increase, but before hare densities reach their peak and food becomes scarce.

Densities of lynx and coyote, the principal predators of hares, had decreased sharply by the winter of 1992-1993 (Boutin et al. 1995), and by 1993 adult hare survival had already increased markedly (Krebs et al. 1995). As snowshoe hare reproduction recovered quickly, from low to peak output in two years, followed soon after by a small increase in hare density in the spring of 1995, the predation-sensitive foraging hypothesis could potentially explain the reproductive changes in this recent cycle. This result differs from that of the Alberta population (Cary and Keith 1979), where reproduction took three years to recover.
Maternal stress

Prolonged exposure to stress during pregnancy affects development, behaviour and fitness in the offspring of some species (Bernardo 1996, Crump and Chevins 1989, Rhees and Fleming 1981) and these results can persist for several generations (Pollard 1986, Mihok and Boonstra 1992). This information is the basis for the maternal stress hypothesis (Boonstra and Singleton 1993, Boonstra et al. 1998a, b). Experimental evidence confirms that hares were physiologically stressed during the decline (Boonstra et al. 1998a), and these increased stress levels were attributed to high predation risk. If negative effects of stress are proven to impair prenatal development, and postnatal growth, survival and fitness, the maternal stress hypothesis could explain the reduced fecundity and smaller young born during the decline, as well as the incremental, rather than immediate increase in fecundity during the low phase. This hypothesis is promising, but requires a number of causal relationships to be quantified, particularly the link between perceived predation risk and stress. The latter might be achieved by comparing the stress response and reproduction of hares from populations exposed to naturally high predation risk, with hares protected from predators, either experimentally reduced or occurring at naturally low density.

Conclusion

Snowshoe hares are capable of having four large litters in a breeding season, yet fail to do so even when food is abundant and predator numbers are relatively low. The similarity between the Yukon and Alberta in the timing of changes in reproduction and the size and age distribution of snowshoe hares relative to fluctuations in density suggests that
these patterns are widespread. What remains to be determined is the cause of the variability in the amplitude and rate of these changes in reproduction.
CHAPTER 3. PRE-WEANING JUVENILE SURVIVAL IN A CYCLIC POPULATION OF SNOWSHOE HARES

INTRODUCTION

It is generally accepted that juvenile recruitment rate strongly influences the growth rate of snowshoe hare populations (Green and Evans 1940, Keith and Windberg 1978, Krebs et al. 1986). The latter two studies agreed that juvenile survival in autumn is highly correlated with rate of change, however there was disagreement over the importance of summer mortality of juvenile hares. Keith and Windberg (1978) argued that the recruitment rate of juveniles to the live-trapped population was set by the reproductive output in the summer and that summer mortality, either before or after weaning, was not correlated with population change. Krebs et al. (1986), however, suggested that recruitment was strongly affected both by changes in reproduction, although this was not directly measured, and by the survival of juvenile hares in the first eight weeks of life. Early mortality of juvenile snowshoe hares can be very high as was reported at the peak in the hare cycle (O'Donoghue 1994).

In the two long-term studies (Keith and Windberg 1978, Krebs et al. 1986), juvenile snowshoe hare survival was estimated from recruitment indices inferred from demographic changes. Here I present the first direct measure of juvenile snowshoe hare survival prior to weaning throughout one snowshoe hare cycle. Snowshoe hares do not appear in live-traps until they are at least 4-6 weeks old, and locating newborn snowshoe hare litters in the wild is virtually impossible. Capturing and maintaining pregnant hares in cages until they gave
birth allowed us to radio-tag snowshoe hares at birth. I compare my results from the first
two years of population increase, 1995 and 1996, with results collected by other researchers
at the same sites during peak (M. O'Donoghue), declining (J. Sovell, B. Kull), and low (C.
Doyle) hare densities from 1989 to 1994, to test if juvenile survival does influence
population growth rate. I also compare proximate causes of mortality and the influence of
litter size and birth weight on pre-weaning snowshoe hare survival.

I propose three reasons why early juvenile hare survival might vary throughout the
hare cycle: i) maternal effect and ii) numerical and iii) functional responses of predators.
First, proposed differences in stress levels (Boonstra et al. 1998a) and foraging behaviour
(Wolff 1980, Hik 1995) influence maternal physiological condition, thereby affecting the
prenatal environment and postnatal nutrition and care (Chapter 2). The probable effects on
the development, health and growth of young hares cause differential juvenile survival.
Second, some of the predators of snowshoe hares (e.g. lynx, coyote, Great-Horned Owl,
Northern Goshawk) exhibit a numerical response to changes in hare density, lagging by one
to two years (Boutin et al. 1995, O'Donoghue et al. 1997). The impact on juvenile survival
will be greatest when the ratio of predators to hares is largest. Third, just as lynx and
coyotes exhibit functional responses to adult hare density (O'Donoghue 1997), some
predators of juvenile hares will respond to the >10-fold variation in the abundance of
juvenile hares (Chapter 2), killing more young hares per predator when leverets are more
abundant.

The predictions based on both i) maternal effects and ii) numerical response of
predators are the same. Juvenile hare survival will be highest during the low phase of the
hare cycle, when predators are rare and food is plentiful, then begin to decrease and reach lowest levels during the decline, when predation risk on mother and offspring is greatest. If juvenile survival is dependent on mothers’ condition, juvenile survival and reproduction parameters will be correlated. The predictions under iii) the functional response of predators is that juvenile survival will be highest during the low phase and lowest at the peak when reproductive output and hare density combine to produce the extremes in leveret density.

**METHODS**

**Juvenile survival estimates**

The same study areas were used for both the reproduction study and the pre-weaning juvenile survival (see Chapter 2, Figure 2.1) except that juvenile survival was only measured on Control 3 in 1989 and 1990. To obtain survival rates from birth, I captured pregnant females within 1 week of parturition and kept them individually in cages until they gave birth (Chapter 2).

The morning after the female gave birth, I removed her from the cage and counted the young. I sexed, measured, and ear-tagged (No. 1 monel tags, National Band and Tag Co., Newport, Kentucky, USA) each newborn and, with the help of an assistant, glued a small radio transmitter (2-2.5g, models SR-1 and SR-2, Biotrack, Wareham, Dorset, England) to the trimmed hair between the shoulder blades. There were three litter groups in 1989, 1990 and 1996, two in 1991 and 1992, and four in 1994 and 1995 (Chapter 2).
Survival was monitored for all litter groups in all years except the fourth litter group in 1994 and 1995.

The mother hare and her litter were returned to the female’s home range where I prepared a litter site. Generally I chose a site in or under deadfall, at the base of a cluster of trees, or in a depression at the base of willows such that the young were protected but the mother could easily find her litter. Snowshoe hares do not burrow or create nests (Severaid 1942, Graf and Sinclair 1987), however the discovery of a natural birth site in 1978 (J. Smith personal communication) and 1995 and similar sites in 1996 (personal observation) suggest that snowshoe hares at least superficially hollow out the birth site. Before placing the young in the litter site, I held the leverets up to their mother who was held in a Tomahawk trap. Once the litter was settled and I opened the trap, the female was allowed to leave when she was ready. She typically stepped up to or over her litter before hopping away.

Each juvenile hare was then radio-tracked daily and visually located at its hiding place or mortality location. Juvenile hares are weaned at approximately four weeks old. The radios generally had ranges of 300 m on the ground and lasted ~6-12 weeks depending on the battery size. The radios usually fell off within 2 to 4 weeks. However, as weaning approached, and with it the risk of dispersal, some animals were trapped to retrieve the radio.

**Determination of proximate causes of mortality**

Necropsies were performed when there was even a partial carcass found. This examination allowed me to confirm whether the animal died of starvation or exposure, or
was killed, and helped to distinguish between predators. Hares that died of starvation had completely empty stomachs and often had blood in the little fat that remained. Hares were categorized as “predation” if the stomach contained milk and there was signs of trauma. Small mammal predators generally attack the rear or neck of their prey and puncture wounds corresponding to teeth and claws were usually clearly evident. Where bones were chewed, there was a rough edge. Sciurids sometimes consume the brains of their prey first, caching or leaving the remainder of the carcass (review in Callahan 1993). Avian predators use the bones to pull the carcass inside out, then pick the bones clean. Whitewash, pellets, feathers and plucking sites helped to distinguish between avian predators (C. Doyle and C. Krebs, unpublished key).

**Calculation of the functional response of red squirrels**

Red squirrels (*Tamiasciurus hudsonicus*) were the primary predator on young hares (O’Donoghue 1994, this study) and they accounted for up to 25% of all mortalities. If red squirrels exhibit a functional response to the density of leverets, this small predator could differentially influence population growth rates throughout the cycle. To calculate the per capita kill rate of juvenile hares by red squirrels in the first 10 days of life, I used the proportion of radio-tagged juvenile hares killed by red squirrels pooled over all grids, and the pooled red squirrel densities for Controls 1 and 4. I used Control grids 1 and 4 because there was a complete record for red squirrel densities on both grids for all years corresponding to this study. Leveret density was calculated for each litter group in each year by multiplying the mean litter size by the adult female hare density in the spring.
Juvenile recruitment to independence

I calculated recruitment rates by multiplying the mean litter size for each litter group (Chapter 2) by the survival rate for that litter group and summed over the breeding season for each year. I estimated the means and standard errors of mean recruitment for each year based on the variance of the products of the components using the following equations:

\[
\mu_{XY} = \mu_X \mu_Y
\]

\[
\sigma^2_{XY} = \sigma^2_X \mu^2_Y + \sigma^2_Y \mu^2_X + \sigma^2_X \sigma^2_Y
\]

(where \( \sigma_{XY} \) is the standard error of the product of litter size and survival rate, X and Y, with means \( \mu_X \) and \( \mu_Y \) and standard errors \( \sigma_X \) and \( \sigma_Y \), respectively).

Statistical analysis

All survival analyses and correlations were performed using Statistica\textsuperscript{\textregistered} (StatSoft 1995). Survival rates were estimated to 30 days, the mean weaning period, using the product-limit (Kaplan-Meier) survival analyses so that I could censor animals that were lost, whose transmitter fell off or that survived beyond the end of the study. To test for differences among multiple years and litter groups, I compared the Kaplan-Meier survival curves using log-rank tests. As the majority of the juvenile hares either died or lost their radio-transmitter by the third week, the logistic regressions (SPSS\textsuperscript{\textregistered}, SPSS 1995) were performed using survival rates to 14 days. I used Pearson’s product-moment correlation coefficient to test the relationship between birth weight and litter size. As Spearman’s rank correlation coefficient is less sensitive to outliers, I used these analyses to test for
relationships between juvenile survival and other demographic factors, correcting for small sample sizes using critical values reported in Zar (1984).

To obtain a density estimate for hares for each year, I averaged the spring density estimates provided by the Kluane Project [average of the program CAPTURE (Otis et al. 1978) and Jolly-Seber method (Seber 1982)] for the Control 1, Control 2 and Control 3 grids (Krebs et al. unpublished data) to provide an overall estimate for the entire valley.

RESULTS

Survival rates

Survival by sex

A total of 561 newborn snowshoe hares from 153 litters were radio-tagged over all seven years. There were only six animals for which sex could not be determined and 13 animals from 1992 for which fates were not delineated by sex. Of the remaining 542 animals, an equal number of males and females (n=271 each) were radio-tagged and, as 30-day survival did not differ between the sex classes (Z=0.253, df=1, p=0.80), I pooled them. I included all 561 radio-tagged animals in the subsequent survival analyses.

Survival by location

Survival estimates were not available for all grids in all years so I tested for differences in 30-day juvenile snowshoe hare survival among the different grids for each year in which multiple grids were used (1994-1996). Sample sizes in 1992 were too small to permit this comparison and only off grid areas were used for Litter 1 in 1994. There
were significant differences in survival rates among grids for all litter groups in 1996 (Figure 3.1; for log-rank results see Appendix 5) but not in 1994 or 1995, with one exception. In 1994, the Control 3 survival rate was based on the death of a single litter of four young resulting in the significant difference among the grids. The survival rate of the remaining grids did not differ. Survival rates for Control 3 were generally lower than for other grids, but this trend was not present for all litter groups in all years. Overall, there appeared to be no consistent pattern in survival across years among the grids, so for all other analyses I pooled all grids assuming similar variability also occurred within grids.

Survival by year and litter group

Survival estimates to 30 days for juvenile snowshoe hares varied significantly among litter groups in four of the seven years (1989, 1990, 1992, 1994; Table 3.1; for log-rank results see Appendix 6). In these years, juveniles born in the second litter of the summer tended to have the lowest survival (0-22%). As there was a litter group effect, I compared among years for each litter group separately. There was a significant difference in juvenile survival among years for all litter groups (Table 3.1; for log-rank results see Appendix 7). Juvenile hares born during the peak and decline phases had consistently lower survival rates than juveniles born during the late low and early increase phases, with the single exception for Litter 1 in 1989 when survival was higher than in any other year. The individual Kaplan-Meier curves on which the log-rank tests were calculated are shown in Appendix 8, for each year and litter group.
Figure 3.1. Inter-grid comparison of 30-day juvenile snowshoe hare survival for Controls 1, 3, 4 and off grid for 1994 through 1996. All grids were not used for all litter groups in all years. Standard errors are indicated. There were significant differences in survival rates among grids for all litter groups in 1996 but not in either 1994 or 1995, with one exception (see text for details).
Table 3.1. 30-day survival estimates for juvenile snowshoe hares by litter group for each year. Standard errors of the survival estimates are shown. Sample sizes indicate the number of hares followed for each time period. There was no third litter in either 1991 or 1992 and juvenile survival was not measured for the fourth litter in 1994 or 1995. Log-rank tests were used to compare among litter groups within each year (column: litter) and among years for each litter group (row: year). Significant differences are indicated as *p<0.05 and ***p<0.001.

<table>
<thead>
<tr>
<th>phase of cycle</th>
<th>Litter 1</th>
<th>Litter 2</th>
<th>Litter 3</th>
<th>Litter groups pooled</th>
<th>n</th>
<th>litter</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989 peak</td>
<td>0.73 ±0.13</td>
<td>0.22 ±0.09</td>
<td>0.18 ±0.12</td>
<td>0.33 ±0.07</td>
<td>46</td>
<td>***</td>
</tr>
<tr>
<td>1990 peak</td>
<td>0.27 ±0.13</td>
<td>0.13 ±0.05</td>
<td>0.51 ±0.11</td>
<td>0.27 ±0.05</td>
<td>76</td>
<td>***</td>
</tr>
<tr>
<td>1991 decline</td>
<td>0.47 ±0.12</td>
<td>0</td>
<td>21</td>
<td>--</td>
<td>0</td>
<td>0.20 ±0.09</td>
</tr>
<tr>
<td>1992 decline</td>
<td>0</td>
<td>9</td>
<td>0</td>
<td>4</td>
<td>--</td>
<td>0</td>
</tr>
<tr>
<td>1994 low</td>
<td>0.50 ±0.22</td>
<td>0.37 ±0.08</td>
<td>0.66 ±0.07</td>
<td>0.54 ±0.06</td>
<td>123</td>
<td>***</td>
</tr>
<tr>
<td>1995 increase</td>
<td>0.71 ±0.11</td>
<td>0.61 ±0.07</td>
<td>0.60 ±0.09</td>
<td>0.63 ±0.05</td>
<td>99</td>
<td></td>
</tr>
<tr>
<td>1996 increase</td>
<td>0.61 ±0.08</td>
<td>0.54 ±0.06</td>
<td>0.56 ±0.07</td>
<td>0.56 ±0.04</td>
<td>166</td>
<td></td>
</tr>
</tbody>
</table>

year       ***    ***    ***
Total juvenile survival in each year was recalculated by pooling across litter groups (Table 3.1). Pre-weaning juvenile survival was positively correlated with population growth rate (r=0.86, n=7; Figure 3.2a), survival of adult hares (r=0.93, n=7; Figure 3.2b) and reproductive output of the same year (r=0.86, n=7; Figure 3.2c), and negatively correlated with density of the snowshoe hare population in the previous spring (r=-0.89, n=7; Figure 3.2d).

**Potential biases of survival estimates**

We lost the radio-signal for 5-21% of all radio-tagged hares in each year and these individuals were treated as censored data. It was unlikely that the juveniles less than three weeks of age would have dispersed, and the survival estimates would be biased if these censored hares either all died or all survived to 30 days (e.g. radio malfunction). To test this bias, I compared Kaplan-Meier curves between the original censored data and these two possibilities (Figure 3.3). I pooled all litter groups within years for this comparison. In most years, there was little discrepancy between the original survival curves and the projected range. However, in 1991, 8 of the 38 (21%) radio-tagged hares went missing, seven of those in the first week, suggesting that the original survival rate might actually have been over- or underestimated by up to 10% in this year. Most losses after the third week (n=167) were probably due to dispersal, since hares that survived to this age had a 98% chance of surviving to the end of the monitoring period.
Figure 3.2. Correlation results between pre-weaning juvenile hare survival and population growth rate, adult hare survival, reproductive output and hare density in the previous year. Juvenile survival was positively correlated with population growth rate ($r=0.86$, $n=7$), survival of adult hares ($r=0.93$, $n=7$) and reproductive output of the same year ($r=0.86$, $n=7$), and negatively correlated with density of the snowshoe hare population in the previous spring ($r=-0.89$, $n=7$).
Figure 3.3. Calculated Kaplan-Meier survival curves treating missing animals as either censored, all dead or all surviving to 30 days. Survival rates were pooled across all litter groups in each year. Censored animals produced little bias in any year, except 1991 (see text for details).
Life history tests

Birth weight and litter size are correlated ($r=-0.19$, $n=192$) and these factors are influenced by year and litter group (Chapter 2). When each parameter is entered separately into a logistic regression model, the results are significant for all parameters. However, when parameters in a logistic regression model are correlated, the results can be difficult to interpret (Zar 1984). It was necessary, then, to use two combinations of the four parameters in forward step-wise logistic regression models to isolate how much each parameter contributed to the model. In a model with year, litter group, litter size and birth weight, year was the only factor that contributed significantly to the improvement of the model (Table 3.2a). As the remaining factors varied with year (Chapter 2), I also looked at how much each factor would contribute to a model without year included. In a forward step-wise regression, all factors significantly improved the model with birth weight providing the most information, followed by litter size and lastly litter group (Table 3.2b). However, when trying to determine if 14-d survival was related to birth weight or litter size within a particular litter group and year, I found no significant interactions. This suggested that either only timing of birth was critical, the year and litter group in which a hare was born, or that by breaking the model down and adding many parameters into the model, I lost the power to detect any real differences.

Fates of juvenile hares

The largest proportion (44.4%; $n=249/561$) of all radio-tagged juvenile hares was killed by predators or died of exposure or starvation. Many of the juvenile hares survived
Table 3.2. Forward step-wise logistic regression results for the influence of neonate birth weight and litter size on pre-weaning juvenile survival of snowshoe hares. In a model (a) with year, litter group, litter size and birth weight, year was the only factor that contributed significantly to the improvement of the model. The correlation among the parameters made it difficult to determine the relative importance of the each factor within year. In model with year removed (b), all parameters improved the model. Birth weight provided the most information, followed by litter size and litter group. * indicates a significant improvement to the model.

<table>
<thead>
<tr>
<th>parameter</th>
<th>change in $\chi^2$</th>
<th>change in df</th>
<th>change in p</th>
</tr>
</thead>
<tbody>
<tr>
<td>year</td>
<td>61.87</td>
<td>5</td>
<td>&lt;0.001*</td>
</tr>
<tr>
<td>birth weight</td>
<td>3.50</td>
<td>1</td>
<td>0.06</td>
</tr>
<tr>
<td>litter size</td>
<td>0.22</td>
<td>1</td>
<td>0.64</td>
</tr>
<tr>
<td>litter group</td>
<td>4.43</td>
<td>2</td>
<td>0.11</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>parameter</th>
<th>change in $\chi^2$</th>
<th>change in df</th>
<th>change in p</th>
</tr>
</thead>
<tbody>
<tr>
<td>birth weight</td>
<td>10.80</td>
<td>1</td>
<td>0.001*</td>
</tr>
<tr>
<td>litter size</td>
<td>4.19</td>
<td>1</td>
<td>0.04*</td>
</tr>
<tr>
<td>litter group</td>
<td>5.05</td>
<td>2</td>
<td>0.08</td>
</tr>
</tbody>
</table>
until either their radio fell off, they reached weaning age or the end of the study (39.9%; n=224/561). Less than 10% (n=53) of all radio-tagged hares went missing and there were only eleven (2.0%) juvenile hares whose fate was undetermined (e.g., the radio was found but it was unclear whether the hare had been killed or the radio had fallen off).

**Proximate causes of mortality**

Over 97% of all mortalities in each year occurred in the first 14 days after birth except in 1994 (73%; 33/45) and 1995 (89%; 32/36). Predation was the leading cause of death, accounting for 80.2% (n=219/273) of all mortalities (Table 3.3). I attributed the largest proportion of these losses (28%, n=62/219) to red squirrels (Table 3.4). If I observed a red squirrel with the carcass or radio, or if the carcass or radio was in a red squirrel tree (defended by red squirrel or nest/midden associated with tree), midden, or hole, the kill was categorized as “suspected red squirrel”. Often the necropsy or chew marks on the radio supported this classification.

An additional 26% (n=56/219) of juvenile hare carcasses or radios were found in trees. It is likely that many of the deaths in this category were due to red squirrels, as the carcasses and radios were found in similar locations as those in red squirrel trees, stuffed in the crook of a branch high up in the tree. The potential that some of the radios found in trees were left behind by an avian predator or scavenger, however, cannot be ruled out. I observed several red squirrels consuming cached carcasses, moving carcasses within and between trees, and cleaning and caching radios in 1995 and 1996. We witnessed red squirrels carrying freshly killed juvenile hares up spruce trees on two separate occasions. In
Table 3.3. Proximate causes of mortality of juvenile snowshoe hares prior to weaning for all years. The phase of the hare cycle is indicated. Predation was the leading cause of death in all years except 1991. All grids and all litter groups were pooled for each year.

<table>
<thead>
<tr>
<th>Cause of death (%)</th>
<th>peak</th>
<th>decline</th>
<th>low</th>
<th>increase</th>
<th>all years</th>
</tr>
</thead>
<tbody>
<tr>
<td>Predation</td>
<td>80</td>
<td>89.3</td>
<td>15.4</td>
<td>62.5</td>
<td>91.1</td>
</tr>
<tr>
<td>Exposure/starvation</td>
<td>0</td>
<td>1.8</td>
<td>80.8</td>
<td>25</td>
<td>0</td>
</tr>
<tr>
<td>Unknown cause</td>
<td>20</td>
<td>5.4</td>
<td>0</td>
<td>12.5</td>
<td>8.9</td>
</tr>
<tr>
<td>Human related</td>
<td>0</td>
<td>3.6</td>
<td>3.8</td>
<td>0</td>
<td>2.8</td>
</tr>
<tr>
<td>n</td>
<td>30</td>
<td>56</td>
<td>26</td>
<td>8</td>
<td>45</td>
</tr>
</tbody>
</table>
Table 3.4. Known and suspected predators of juvenile snowshoe hares prior to weaning for all years combined. Values represent the proportion of all predation events.

<table>
<thead>
<tr>
<th>Predation deaths</th>
<th>Proportion (%)</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red squirrel</td>
<td>28.3</td>
<td>62</td>
</tr>
<tr>
<td>Arctic ground squirrel</td>
<td>10.5</td>
<td>23</td>
</tr>
<tr>
<td>Short-tailed weasel</td>
<td>4.1</td>
<td>9</td>
</tr>
<tr>
<td>Unknown small mammal</td>
<td>5.5</td>
<td>12</td>
</tr>
<tr>
<td>Carcass or radio in a tree</td>
<td>25.6</td>
<td>56</td>
</tr>
<tr>
<td>Great-horned Owl</td>
<td>4.1</td>
<td>9</td>
</tr>
<tr>
<td>Northern Goshawk</td>
<td>4.1</td>
<td>9</td>
</tr>
<tr>
<td>Boreal Owl</td>
<td>1.8</td>
<td>4</td>
</tr>
<tr>
<td>Red-tailed Hawk</td>
<td>0.5</td>
<td>1</td>
</tr>
<tr>
<td>Unknown avian</td>
<td>5.0</td>
<td>11</td>
</tr>
<tr>
<td>Unknown predator</td>
<td>10.5</td>
<td>23</td>
</tr>
</tbody>
</table>
the first case, I had located the hare alive just one hour before. The second was a 10-day old hare, weighing 110g, which the red squirrel had considerable trouble carrying up the tree, settling for a branch only a meter from the ground (J. Hughes, personal communication). The necropsy revealed considerable trauma to the front leg and a severely dislocated shoulder.

Arctic ground squirrels (*Spermophilus parryii*) were credited with 10.5% (n=23/219) of all predator kills, taking many of the radios or hare carcasses into their burrows. Two carcasses were left essentially intact at burrow entrances, with only the brains partially eaten. In one instance, a ground squirrel killed two littermates on subsequent days and carried them to the same burrow system. After digging up a small section, I discovered that this was the ground squirrel’s natal burrow where seven hairless ground squirrel pups were nested. I returned for the radios several weeks later, after the ground squirrels had emerged, to find the nest gone and the burrow rearranged. Short-tailed weasels (*Mustela erminea*) were suspected to have killed nine hares (4.1%), all in 1994, with one direct observation (C. Doyle, personal communication) of a weasel guarding the opening of the hole where it had dragged the carcass of a juvenile hare. Twelve small mammal predation kills (5.5%) could not be positively assigned.

Avian predators killed 34 juvenile hares, 15.5% of all predation deaths. Known predators included the Great-Horned Owl (*Bubo virginianus*), Northern Goshawk (*Accipiter gentilis*), Boreal Owl (*Aegolius funereus*) and Red-tailed Hawk (*Buteo jamaicensis*). Eleven deaths could not be attributed to any particular avian predator. We did not record any lynx (*Lynx canadensis*), coyote (*Canis latrans*), or red fox (*Vulpes*
kills of juvenile hares, however if juvenile hares were taken by these predators, it is likely that either the radio did not survive digestion or that the predator moved out of range. In either case, the hares would have been classified as missing and, at most, these large carnivores would account for 16% of all predation deaths. Death due to exposure or starvation represented 9.9% (n=27/273) of all mortalities, the majority (n=21) of which occurred in 1991, the first year of the decline.

There was the possibility that the hares were scavenged after they had already died or been killed. A scavenging experiment was conducted in 1990 (O'Donoghue 1994). The results from this experiment suggested that 1-day scavenging rates were 17.5% (7/40) and 43.5% (10/33) for juvenile hares simulated to have died from exposure and predation, respectively. This rate could imply that some, but not all, hares that died were scavenged and thus the actual cause of death incorrectly classified. Given that the “exposure” carcasses were placed in locations similar to hare hiding spots, however, it is possible that the squirrels that scavenged these carcasses would have killed the young hares if they had actually been alive. It also seems unlikely that a large avian or mammalian predator would leave behind such a small prey item, making small predators the most likely predators. In addition, from the necropsies, I could determine whether the hare had died from exposure or starvation first, or had been killed.

**Functional response of red squirrels**

Red squirrels showed a functional response to changes in density of leverets, particularly in the second litter of the year (Figure 3.4). Kill rates were highest at peak hare
densities (1.48 hares/ha) in 1990 and lowest in 1994 when hare densities were lowest (0.08 hares/ha). The maximum kill rate of 0.4 leverets/red squirrel/10 days was observed in Litter 2 in 1990. The functional response for the first litter of the year was weaker than in the other two litters. No leverets were killed by red squirrels in Litter 1 in either 1989 or 1991. I did not try to fit a curve to the data (as per Holling 1959) as there were, at most, seven points per plot.

**Juvenile recruitment to independence**

The number of juvenile hares per female that survived to independence varied nearly 10-fold over the course of the cycle (Figure 3.5). Recruitment rates dropped from an average of 4.7 young per female in 1989, the first year of the peak, to 0 young per female by the late decline in 1992. Then, within two years, recruitment levels jumped to 8 young per female and reached their highest level of 9.7 young per female the following year, the first year of the increase. Mean recruitment rate was highly correlated with the population growth rate ($r=0.88$, $n=7$; Figure 3.6).

**DISCUSSION**

Pre-weaning survival rates of juvenile snowshoe hares were highly variable among litter groups and among years. The difference among years appeared to be related to the hare cycle, with lowest survival occurring during the decline and highest survival occurring during the increase phase of the cycle, suggesting that juvenile survival may be an important factor in the changes in population densities. After discounting the cases where the cause of death was unknown, predation accounted for up to 80% of early mortality in
Figure 3.4. Functional response of red squirrels to changes in leveret density for each of the three litter groups. The highest density of leverets produced in Litter 2, due to large mean litter sizes, probably contributed to the strong functional response observed. Small litter sizes and the naivété of red squirrels early in the hare breeding season, combined with the high proportion of non-predation deaths of leverets in 1991, were the probable causes of the weak functional response seen in Litter 1.
Figure 3.5. Changes in number of juvenile snowshoe hares weaned per female across the snowshoe hare cycle. Mean values (●) for each year (± S.E.) were calculated by combining mean litter sizes and 30-day juvenile survival rates by litter group over the breeding season.
Figure 3.6. Correlation between mean annual recruitment rate and population growth rate. The two factors were strongly correlated ($r=0.88$, $n=7$).
population rate of change \((t+1/t)\)
most years. Small mammalian predators, particularly red and arctic ground squirrels, were attributed with 40% of all kills. Survival was most closely tied to the litter group and year in which a hare was born and if there were any trade-offs between survival and birth weight or litter size, they were overshadowed by the strong influence of the timing of birth. There was a large change in the number of juvenile hares that survived to independence, owing to concurrent changes in both reproductive output and pre-weaning juvenile survival, and this change in recruitment levels was highly correlated with changes in population growth.

**Survival rates**

Juvenile snowshoe hare survival prior to weaning varied considerably both within and across years. The correlative association with other demographic parameters supports the conclusion that changes in juvenile survival reflect cyclic dynamics. The cyclic trend is also evident in the differences in the proximate cause of death throughout the cycle. In the decline phase, the majority of deaths (80.8%) were due to starvation or exposure, however predation was the main cause of death in all other phases of the cycle. Sampling effort was very similar between 1989 (peak), 1991 (decline) and 1994 (low), and yet this difference in the causes of death emerged, suggesting that there was a qualitative difference in the juveniles born in the decline year, 1991, relative to other years. Juvenile hares born in 1991 weighed 5-33 % less at birth (Chapter 2) than hares born in any other year, so the differences in the size of newborn hares among years were concurrent with the observed differences in survival across the cycle. The influence of the size at birth on survival was implied by the primary significance of birth weight in the logistic regression model when
year was removed. Owing to the difficulty in teasing the related factors apart, however, the influence of birth weight on survival through the hare cycle could not be confirmed. The variability in survival rates among litter groups also differed across the cycle, being most pronounced at peak and declining densities. I suggest that the cause of this variability is related to changes in predation risk across the cycle.

Keith and Windberg (1978) also estimated very low survival to 45-days (0.15, 0.05) in 2 of 3 decline years at their Halls site, and moderate survival during the increase (0.35, 0.31). Although Keith and Windberg did not find a correlation between early juvenile survival and population growth rate at their Rochester site, early juvenile survival estimates were also low (0.15, 0.21, 0.14) in 3 of 4 years of the first decline (but not the subsequent decline) and, as at the Halls site, moderate during the increase (0.53, 0.33, 0.42). However, contrary to our results, survival estimates were highest at peak hare densities at both sites in Alberta.

It seems unlikely that changes in juvenile survival resulted entirely from chance events. If Control 3 hares suffered consistently higher mortality, the survival estimates would have been inflated in years in which multiple grids were used, during the low and early increase. Yet when I calculated survival estimates across the cycle looking only at Control 3, a similar trend remained (Figure 3.7), although the pattern was less convincing. Low sample sizes, particularly in 1994, reduced my power to detect statistical differences. Obviously, equal representation of multiple sites for all years would have been more desirable, yet I believe the trends exhibited here imply a cyclic influence and certainly warrant further study.
Life history factors

There was no conclusive evidence for life history trade-offs between juvenile hare survival and either birth weight or litter size. Rather it appeared that the year and litter group in which a hare was born were the best predictors of its survival (see also O'Donoghue 1994). However, as all the factors were correlated, the smaller size of young hares in some years may put them at greater risk to exposure or predators.

Proximate causes of mortality

The combined impact of exposure and starvation resulted in the lowest juvenile survival rates during the decline. Since predation was the primary cause of mortality in all other phases of the cycle, we must look to the differences in the predator community and predation rates to explain why survival rates differed among these years. Recall the predictions: first, if numerical changes in predators influence juvenile survival, the impact will be greatest when the ratio of predators to hares is largest, during the decline, and will be lowest during the low. Second, if predators exhibit a functional response to changing leveret density, kill rates will increase with increasing leveret density.

Impacts of changes in predator density

Although numerical changes in any predator could have potentially influenced juvenile hare survival rates, small mammals were the main predators of juvenile hares and so would likely have had the most impact. Densities of all predators of juvenile hares were taken from Boutin et al. (1995). Red and arctic ground squirrel predation continued to be
Figure 3.7. 30-day juvenile survival for Control 3. The trend of juvenile survival throughout the cycle is similar, but weaker, than that observed when all grids were combined. The high variability in survival rates, particularly at peak hare densities in 1989 and 1990, as well as small sample sizes, particularly in 1994, contributed to the lack of significance in survival rates among years.
important throughout the cycle, as they were at peak hare densities (O'Donoghue 1994). Ground squirrel densities fluctuated in relative synchrony with the hare cycle, and most of the kills by this predator occurred during increasing and peak densities of both species. Red squirrel densities were independent of the hare cycle but were closely tied to white spruce cone crops, with maximum densities occurring in 1994 (3.2 squirrels/ha) on most areas owing to a mast cone year in 1993.

Weasel densities were also independent of the hare cycle and reached peak densities in 1994 due to the high densities of voles (*Microtus* sp.) in the previous year. The higher densities of weasels explained the increase in weasel kills in 1994. However, despite high numbers of both red squirrels and weasels in 1994, juvenile hare survival was still >15% higher on average than it was at peak hare densities in 1989 and 1990. Evidence of the impact of small mammal predation on juvenile hare survival and hare populations comes from a study of a non-cyclic population of snowshoe hares on Jacquot Island in the same area as this study (Zimmerling 1993, Jardine 1995). The >25% higher survival of juvenile hares on the island compared with the mainland was responsible for faster turnaround and higher population growth rate following a decline in hare density. The difference in survival was attributed to the absence of ground squirrels and rarity of red squirrels (e.g., in 1994, 0.2/ha on the island compared to a minimum of 1.75/ha on the mainland).

Mammalian and avian predators undergo cyclic numeric changes, lagging 1-2 years behind hare densities (Boutin *et al.* 1995). Thus, we would expect to see the proportion of these predation events corresponding to predator density, with the majority of these deaths occurring during the peak and the decline phases. It was clear that even though predator
densities were high during the decline, predation was not the critical factor in the survival of young hares at this time. Since large mammal predation could not be estimated, I could not test how changes in the densities of these predators affected juvenile hare survival. However I have better information for avian predators.

Contrary to the above prediction, fewer avian kills of juvenile hares were recorded at the peak (2/30 and 3/56 of all mortalities) than during the low (11/45) and early increase (9/36 and 8/72) phases of the cycle. I suspect that this was due, in part, to the large and local territories held by raptors and the disproportionate numbers of grids used during the different years. Perhaps by using multiple areas in 1994 through 1996, we covered more avian territories and increased the chance of detecting more kills even though densities of raptors was low (Boutin et al. 1995). In fact, there was only one case in 1989 where two different raptor species were recorded killing juvenile hares on the same grid.

The only raptor for which an increase in density corresponded to an increase in the number of juvenile hare kills was for the Boreal Owl. As with the weasel, Boreal Owl densities increased owing to high densities of small mammals in 1992 and 1993 (Boutin et al. 1995) and, despite low hare densities, 1994 and 1995 were the only two years in which leverets were killed by this predator.

That we should see more juvenile hares killed by avian predators during the peak and decline was supported by diet analysis of raptors across the cycle (F. Doyle, unpublished data). Juvenile hares appeared in the diet of raptors much more frequently in 1990 (in 28% to 56% of all pellets for Red-tailed Hawks, Northern Harriers and Northern Goshawks), than in 1993 or 1994 when juvenile hares were essentially absent from their
diet. Pellet analysis also revealed high predation rates on leverets by Great-Horned Owls in 1989 and 1990 (Rohner and Krebs 1996). Leverets appeared in the owls’ diet a few days after the mean parturition date of hares for both Litters 1 and 2. At these times, the owls preferentially preyed on hares <14 days old, relative to adult and older juvenile hares, and this differential predation, along with the apparent increase in other avian predation, could potentially limit juvenile recruitment at peak densities.

Overall, using radio-telemetry, I was only able to detect corresponding differences in the proportion of juvenile hares killed relative to predator densities for weasels and Boreal Owls. These results suggest that the changes detected in juvenile hare survival across the cycle were not caused by the changes in the densities of their main predators. However, the increase in the proportion of juvenile hares in the diets of avian predators may point to a functional response of these predators to changes in leveret density.

**Functional responses of red squirrels**

A functional response to changes in leveret density was clearly shown for red squirrels for Litters 2 and 3. The strongest response occurred in Litter 2, when a 4-fold increase in leveret density in 1990, resulted in a proportional increase in the kill rate by red squirrels. Leveret density was maximal during this litter group owing to the relatively larger litter sizes produced at this time, compared with earlier or later in the season, and therefore the risk of detection by squirrels was probably higher. The weaker relationship observed for Litter 1 was due to the absence of red squirrel kills in 1989 and 1991. In 1991, 81% (n=21/26) of all leverets in both litters died from exposure or starvation within four days of
birth, with only one exception (11 days), making these hares unavailable for red squirrel predation. The smaller mean litter size of Litter 1 relative to the other litter groups and the probable naivété of the red squirrels early in the season may have also contributed to this result.

The differential slopes of the functional responses for each litter group correspond to the patterns of juvenile survival within years. In the four years where there was a significant difference in juvenile survival among litter groups, Litter 2 survival was consistently lower than in the other litter groups, with only one exception (Table 3.1).

How red squirrels find juvenile hares is unknown. Whether the functional response to increasing leveret density is a result of a general increase in the opportunistic kill rate by all red squirrels or whether individual squirrels are more efficient predators is difficult to determine. However, at peak hare densities, when red squirrel kill rates were highest, littermate survival was not independent during the first five days (O'Donoghue 1994). This period corresponds to the highest susceptibility of leverets to red squirrel predation. Up to ~10 days old leverets remain motionless in their hiding spot, moving rarely except once each evening to nurse (O'Donoghue and Bergman 1992, this study). Red squirrels are known predators on song bird nests (e.g., review in Paton 1994, Campbell 1995) and have been shown to increase their search rate and efficiency after finding the first nest (S. Pelech, unpublished data). The lack of independence of littermates, and evidence from Pelech's nest predator study, suggests that not all squirrels find or search out the young hares; however, those squirrels that do, become very effective at finding other hares. An example
of this possible searching behaviour occurred in 1996, when one red squirrel was suspected of killing all nine leverets from two separate litters released within its territory.

The hypothesis that some red squirrels actively search for prey after an initial encounter could be tested using a manipulative experiment. Using the same technique for measuring juvenile hare survival as this study, a range of leveret densities could be created within known red squirrel territories by selecting the number of hare litters for release on each territory. By recording the fate and location of all radio-tagged hares, the researcher could continuously track leveret densities. This would be best accomplished at near peak hare densities to capitalize on high hare densities, while avoiding the decline when predation is less of a factor. The use of remote cameras can be an effective way to observe predation events (e.g., marbled murrelets, J. Bradley, personal communication), and could be used to examine predator behaviour.

**Change in recruitment levels**

The change in the number of juvenile hares that survived to weaning was a combination of both the number of young that were produced and the number of those young that survived. These changes coincided with each other and resulted in a 10-fold difference in the number of young per female that were recruited to independence across the cycle. In a demographic model of the snowshoe hare cycle at Kluane, we reported strong influences of recruitment rates on the population growth rate (Haydon et al., submitted). The model suggested that the rate of change in the snowshoe hare population was most sensitive to changes in post-weaning juvenile survival and equally sensitive to changes in
pre-weaning juvenile survival, reproduction and adult survival. The combination of reproduction and pre- and post-weaning juvenile survival accounted for most of changes in population growth rate and equates to the recruitment indices described by Krebs et al. (1986) and Keith and Windberg (1978). However, contrary to the idea that recruitment is due *solely* to changes in reproduction and autumn survival of juvenile hares (Keith and Windberg 1978), these results support the hypothesis that pre-weaning juvenile hare survival also strongly influences snowshoe hare population dynamics (Krebs et al. 1986).

I suggest that the changes in juvenile survival rates across the cycle were due to two primary factors. First, the changes in juvenile hare survival rates were due to the functional response of predators, particularly red squirrels and perhaps Great-Horned Owls (Rohner and Krebs 1996), to changes in leveret density. Second, the changes in juvenile survival were the result of a physiological change in the mother and her ability to provide for her offspring. A shift in the primary cause of death of newborn hares, from predation to exposure and starvation during the decline, is consistent with the stress hypothesis (Boonstra and Singleton 1993, Boonstra *et al.* 1998a). An increase in the levels of stress hormones in 1991 and 1992, possibly due to prolonged predation risk, reportedly affected the immune system and caused a higher incidence of anemia in snowshoe hares during the decline. Thus, the prenatal environment in which the young hares developed likely differed throughout the cycle, potentially affecting the size, number and physiological condition of neonates (Boonstra *et al.* 1998a). Newborn mammals also rely on the natural antibodies in their mothers’ milk, so if the mothers’ immune system was suppressed during the decline,
their offspring may also have been at a disadvantage after birth. This maternal effect across the cycle, both during development and after birth, needs to be addressed experimentally.

The prediction that numerical changes in predator density would affect juvenile survival was inconclusive. I predicted that the highest mortality would occur during the early part of the decline, when the proportion of predators to hares was high. Although juvenile survival was extremely low at this time, predation was not the primary cause of death. Except for predation by weasels and Boreal Owls, the impact of changing predator density was unclear: As the density of both of these small predators is unrelated to hare density, their effects on hare population growth rate cannot contribute to cyclic dynamics. However the additive impact of predation by these predators and those that do respond numerically to hare density could potentially modify the amplitude and rate of change in recruitment levels, and therefore population growth rate, throughout the cycle.

Conclusions

These results reinforce previous research suggesting that juvenile snowshoe hare mortality rates prior to weaning greatly affect juvenile recruitment (O'Donoghue 1994). The strong correlations between juvenile survival and other demographic parameters also support the hypothesis that changes in these survival rates contribute to the cyclic dynamics of snowshoe hare populations (Krebs et al. 1986). The functional response of some abundant predators, such as the red squirrel, and the preference for young hares by other rarer but larger predators, such as the Great-Horned Owl (Rohner and Krebs 1996), appear to work in concert to slow the population growth rate of hares at peak hare densities. This
increase in predation may allow predator densities to catch up and force the decline of the entire hare population.

It can now hardly be disputed that red squirrels were the critical factor in juvenile hare survival at Kluane. It remains to be determined whether red squirrel predation also occurs with this frequency in other parts of the snowshoe hares' geographical range. As indicated by the research on Jacquot Island, a long-term comparison of pre-weaning juvenile survival between cyclic and non-cyclic snowshoe hare populations, between and within regions, could provide another test for the relative importance of pre-weaning juvenile survival on the population growth rate, and cyclic dynamics, of snowshoe hares.
CHAPTER 4. GENERAL CONCLUSIONS: PRE-WEANING RECRUITMENT OF JUVENILE SNOWSHOE HARES IN A CYCLIC POPULATION

Pre-weaning recruitment of juvenile snowshoe hares changed dramatically over the course of the snowshoe hare cycle at Kluane. The multiplicative effects of cyclic changes in early juvenile survival and natality rate of snowshoe hares combined to produce this variation. The resultant recruitment rate was strongly correlated with the rate of change in the population. I will first summarize the notable findings and conclusions for each component of recruitment and finish with a discussion of the impacts of variable recruitment on the population dynamics of snowshoe hares.

Cyclic changes in reproduction

All reproductive parameters varied simultaneously and were correlated with the rate of change in the hare population. Changes in reproduction preceded corresponding changes in density by two years. Owing to changes in both pregnancy rates and litter sizes, natality was lowest (6.9 and 7.0 young per female) during the decline phase, highest (18.5) during the late low and early increase phase, and then declined (to 12.8) at peak hare densities. A similar but not identical trend emerged for neonatal measurements. The one difference is that the size and weight of neonates continued to improve during the increase, reaching a maximum one year after the peak in reproductive output.

In Alberta, although the lag in density was longer (3 years) than in this study, my results were consistent with those results reported by Cary and Keith (1979) for another
cyclic population of snowshoe hares. Yet we differ in our opinion about the cause of the changes in reproduction. Cary and Keith concluded that reproduction was determined by over-winter weight loss. However it is unlikely that the decrease in reproduction was due to limited availability of food, as reproduction started to decline during the increase before food should have been limiting. Rather, my results suggest a probable indirect effect of predators through a combination of behavioural changes affecting accessibility to food resources (Wolff 1980, Hik 1995) and fluctuating stress levels associated with perceived predation risk (Boonstra 1998a, b). Some predators respond quickly to changes in hare density and, as seen for coyotes (O’Donoghue 1997), can reach peak efficiency before hare densities are highest. The virtually identical changes between neonate sizes and other reproductive characteristics support the hypothesis of qualitative physiological differences in the mother throughout the cycle.

**Cyclic changes in pre-weaning juvenile survival**

Pre-weaning juvenile survival also varied cyclically in this population of snowshoe hares. Predation was the primary cause of death in all phases of the cycle except the decline, when starvation and exposure claimed most of the young hares. Survival was low and highly variable at peak hare densities, varying as much as 60% within a year but with an average survival rate of approximately 0.3 in each of the two years. Few or no recruits were produced through the decline as survival plummeted to zero in three of the four litters from both years. Juvenile survival had improved considerably to a summer average of 0.54 by the end of the low, but was still variable (0.50, 0.37, 0.66). The second litter fared
poorly as was seen during the peak. By the increase, survival of young hares was consistently high throughout the summer, reaching a maximum average of 0.63 in the first year of the increase and remaining high (0.56) for the second year.

These changes in pre-weaning juvenile survival rates and causes of death were attributed, in part, to a functional response of juvenile hares' main predators, particularly red squirrels, and a change in the pre-natal environment and post-natal nutritional support from the mother. The high incidence of starvation and of mortalities due to exposure during the decline indicates a possible maternal effect, through the combined impact of malnutrition and stress effects. These links need to be examined. Although red squirrels were the only predator for which a functional response was quantified and confirmed, Great-Horned Owls, and other predators, may also change their kill rates relative to the densities of leverets. The potential functional response of Great-horned Owls can be seen in their preference for very young hares (<14 days old) relative to other age classes at peak hare densities (Rohner and Krebs 1996).

**Putting the pieces together: recruitment of juvenile hares to weaning**

The parallel changes in reproduction and pre-weaning juvenile survival combined to produce a 10-fold difference in recruitment of juvenile hares to independence throughout the cycle. Models of demographic changes suggest that the population growth rate is equally sensitive to variation in these two parameters (Haydon et al., submitted). My results support the premise of Krebs et al. (1986), that both reproduction and early juvenile survival strongly influence the population growth rate of snowshoe hares.
Young hares born during the low and early increase phase of the cycle are doubly advantaged. They are large and healthy, and relatively rare. But as hare numbers increase, some predators begin cueing in to the abundance of this prey, and mortality increases. The combination of the high kill rate of young hares and the decrease in reproduction slows the population growth rate at peak hare densities. As the reduction in recruitment allows the predator densities to catch up, predation risk increases for the entire hare population. By the decline, the increased and chronic stress imposed by high predation risk takes its toll on the mother, such that she produces few young and those that are born fare poorly.

To test this hypothesis, a number of components need to be examined. First, we must measure the sub-lethal effects of predators by analyzing the changes in activity budgets of hares and further testing of the stress hypothesis at all phases of the cycle. The link between maternal effects and offspring development, growth and fitness also needs to be quantified. In this way we could better understand why reproduction increases incrementally instead of immediately when predation risk is low. We also need to quantify early juvenile survival and determine the main predators in other habitats and geographical areas. Through such investigations we can test the generality of the cyclic trends observed in this study and determine whether the same, or a different, suite of predators can limit population growth by responding functionally to changing abundance of young hares.
LITERATURE CITED


Severaid, J.H. 1942. The snowshoe hare, its life history and artificial propagation. Maine Department of Inland Fisheries and Wildlife, Augusta, Maine.


Appendix 1. Mean birth weight of newborn hares by year for yearling and older females snowshoe hares. There were no older females in 1992 and only one in 1994.
Appendix 2. Regression of mean birth weight and mean right hind foot length for newborn snowshoe hares using means from all litter groups ($F=502.22$, $df=1,190$, $r^2=0.73$, $p<0.001$).
Appendix 3. Regression plots of mean birth weight and mean right hind foot for newborn snowshoe hares by year and litter group. Each circle represents the mean for one litter.
Birth Weight (g)

LITTER 3
LITTER 2
LITTER 1

1989
1990
1991
1992
1994
1995
1996

Right Hind Foot Length (mm)
Appendix 5. Results of log-rank comparisons among grids for 30-day survival rates by litter group for 1994, 1995 and 1996. Sample sizes are indicated.

<table>
<thead>
<tr>
<th>year</th>
<th>litter group</th>
<th>control grids compared</th>
<th>$\chi^2$ statistic</th>
<th>df</th>
<th>p</th>
<th>number of individuals by grid</th>
</tr>
</thead>
<tbody>
<tr>
<td>1994</td>
<td>1</td>
<td>only off grid used</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>1, 3, 4, off grid</td>
<td>4.79</td>
<td>3</td>
<td>&gt;0.1</td>
<td>11, 18, 7, 10</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>1, 3, 4, off grid</td>
<td>19.40</td>
<td>3</td>
<td>&lt;0.001</td>
<td>27, 12, 7, 4</td>
</tr>
<tr>
<td>1995</td>
<td>1</td>
<td>1, 3</td>
<td>0.648</td>
<td>1</td>
<td>&gt;0.5</td>
<td>6, 11</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>1, 3, off grid</td>
<td>0.065</td>
<td>2</td>
<td>&gt;0.9</td>
<td>15, 13, 21</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>1, 3, off grid</td>
<td>0.582</td>
<td>2</td>
<td>&gt;0.7</td>
<td>14, 10, 7</td>
</tr>
<tr>
<td>1996</td>
<td>1</td>
<td>1, 3</td>
<td>2.55</td>
<td>1</td>
<td>&lt;0.05</td>
<td>18, 21</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>1, 3, 4</td>
<td>11.09</td>
<td>2</td>
<td>&lt;0.01</td>
<td>24, 36, 6</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>1, 3, 4</td>
<td>9.76</td>
<td>2</td>
<td>&lt;0.01</td>
<td>21, 30, 10</td>
</tr>
</tbody>
</table>
Appendix 6. Results of log-rank comparisons for 30-day survival rates among litter groups by year. Sample sizes are indicated.

<table>
<thead>
<tr>
<th>phase of cycle</th>
<th>$\chi^2$ statistic</th>
<th>df</th>
<th>p</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989 peak</td>
<td>13.80</td>
<td>2</td>
<td>&lt;0.001</td>
<td>46</td>
</tr>
<tr>
<td>1990 peak</td>
<td>16.35</td>
<td>2</td>
<td>&lt;0.001</td>
<td>76</td>
</tr>
<tr>
<td>1991 decline</td>
<td>0.338</td>
<td>1</td>
<td>0.740</td>
<td>38</td>
</tr>
<tr>
<td>1992 decline</td>
<td>2.23</td>
<td>1</td>
<td>0.026</td>
<td>13</td>
</tr>
<tr>
<td>1994 low</td>
<td>16.08</td>
<td>2</td>
<td>&lt;0.001</td>
<td>123</td>
</tr>
<tr>
<td>1995 increase</td>
<td>0.736</td>
<td>2</td>
<td>0.692</td>
<td>99</td>
</tr>
<tr>
<td>1996 increase</td>
<td>0.25</td>
<td>2</td>
<td>0.880</td>
<td>166</td>
</tr>
</tbody>
</table>
Appendix 7. Results of log-rank comparisons for 30-day survival rates among years by litter group. Sample sizes are indicated.

<table>
<thead>
<tr>
<th>Litter</th>
<th>$\chi^2$</th>
<th>df</th>
<th>p</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>26.2</td>
<td>6</td>
<td>&lt;0.001</td>
<td>134</td>
</tr>
<tr>
<td>2</td>
<td>64.5</td>
<td>6</td>
<td>&lt;0.001</td>
<td>250</td>
</tr>
<tr>
<td>3</td>
<td>20.2</td>
<td>4</td>
<td>&lt;0.001</td>
<td>177</td>
</tr>
</tbody>
</table>
Appendix 8. Kaplan-Meier 30-day survival curves by litter group for all years. Uncensored data are indicated by symbols and censored data by a cross. All grids were pooled.