Reproductive changes in a cyclic population of snowshoe hares

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Abstract: Reproductive output was estimated for a cyclic population of snowshoe hares (*Lepus americanus*) in the Kluane Lake region of the southwest Yukon Territory. Data collected by five researchers were collated over 8 years (1989–1996). Pregnant hares were captured and held in cages until they gave birth so that reproductive characteristics could be measured. Pregnancy rate, litter size, and neonate size fluctuated significantly throughout the cycle, changes occurring about 2 years before corresponding changes in density. Pregnancy rates were nearly 100% early in the breeding season, but declined up to 20% in the last gestation periods of the year. The number of litters produced in a breeding season varied between two (decline phase) and four (low, early increase phase). Litter size varied among years as well as among litters within a year, larger litters being born later in the breeding season. The body mass and size of newborn hares varied by 5–33% among years. The combined changes in pregnancy rate and litter size resulted in a cyclic change in total reproductive output ranging from a low of 6.9 young per female during the decline phase to a maximum of 18.9 during the second year of the low and early increase phases.

Résumé : Le rendement de la reproduction a été estimé chez une population cyclique de Lièvres d'Amérique (*Lepus americanus*) de la région du lac Kluane dans le sud-ouest du Yukon. Les données recueillies par cinq chercheurs pendant 8 ans (1989–1996) ont été colligées. Des femelles enceintes ont été capturées et gardées en cage jusqu'à la mise bas, ce qui a permis de mesurer les caractéristiques de la reproduction. Nous avons enregistré des fluctuations significatives des taux de grossesse, du nombre de petits par portée et de la taille des nouveau-nés pendant tout le cycle, environ 2 ans avant que ne se produisent les fluctuations correspondantes de la densité. Les taux de grossesse étaient presque toujours de 100 % au début de la saison de reproduction, mais pouvaient baisser d'un fort pourcentage (jusqu'à 20 %) au moment des dernières grossesses de l'année. Le nombre de portées produites en une saison variait de deux (phase de déclin) à quatre (phase du minimum, début de la recrudescence). La taille des portées variait d'une année à l'autre et d'une portée à l'autre au cours d'une année, et c'est vers la fin de la saison de la reproduction qu'apparaissaient les plus grosses portées. La masse et la taille des nouveau-nés variaient de 5–33 % d'une année à l'autre. La combinaison des fluctuations des taux de grossesse et du nombre de petits par portée entraînait un changement cyclique du rendement, passant d'une production de 6,9 petits par femelle durant la phase de déclin à 18,9 petits au cours de la seconde année du déclin et au début de la période de recrudescence.

[Traduit par la Rédaction]

Introduction

The causes of cyclic fluctuations in density of snowshoe hare (*Lepus americanus*) populations have been vigorously debated (Green and Evans 1940; Keith 1983; Trostel et al. 1987; Krebs et al. 1995; Murray et al. 1997; Boonstra et al. 1998*a*, 1998*b*). 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 snowshoe hares in Alberta, Cary and Keith (1979) used necropsy 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 the cycle. Changes in reproduction preceded changes in density by about 3 years. In another study, Krebs et al. (1986) livetrapped snowshoe hares in the Yukon Territory. They did not measure reproductive parameters directly; however, variation in the length of the breeding season and a strong correlation between juvenile recruitment and the rate of population change were observed. Although the results of these studies were at variance concerning the impact of over-winter food resources on the changes in hare density, the similarities in reproductive patterns and juvenile recruitment warranted further investigation.

The objective of this study was to describe reproductive changes spanning 8 years of a snowshoe hare cycle in the Kluane Lake region of the Yukon. We predicted that the changes in reproductive parameters would precede the cyclic changes in hare density by several years, like the changes reported by Cary and Keith (1979) in Alberta. We collected data during increases in hare densities in 1995 and 1996 and compared them with data collected by other researchers in previous years at the same sites. This study is unique because we measured reproduction by following individual hares through pregnancy by means of a capture–release technique that also permitted us to count and measure live young.

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Materials and methods

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

Snowshoe hare populations were monitored via livetrapping throughout the breeding season (April–August) from 1989 to 1996, with the exception of 1993 when reproduction was not measured but livetrapping was conducted in the spring and fall to obtain density estimates. In all years trapping occurred on 36-ha control grids established as part of the Kluane Boreal Forest Ecosystem Project (hereinafter Kluane Project). There were 86 Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin, U.S.A.) on each grid, placed 43 m apart along four evenly spaced rows. In 1992, 1994, and 1995, when hare densities were low, we also set traps in off-grid areas.

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

The protocol for handling and care of adult female and newborn hares has remained consistent for all studies of reproduction associated with the Kluane Project, beginning in 1989 (O'Donoghue 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 of pregnant females was focused around these peak times. We determined the stage of a hare's pregnancy by the body mass and the colour of the lactational tissue, and by palpating the abdomen. Hares estimated to be in the last week of pregnancy were placed in individual 60 × 60 × 120 cm chicken-wire cages (O'Donoghue and Krebs 1992), which provided shelter, a partitioned (spruce branch or burlap sheet) area of refuge, and straw for nesting material. Early in the first season, the cages were placed on the grids near the location where each female was trapped. However, because cages on some grids were disturbed by bears, cages were then located within electrically fenced enclosures at least 200 m from the grids.

Until the females gave birth they were checked, watered, and fed rabbit chow, apples, and natural forage each morning. The morning after they gave birth we removed them from the cage and counted the young. We sexed, weighed, ear-tagged (No. 1 Monel tags), and measured the right hind foot length of each newborn. Each female hare and litter were immediately returned to her home range, where she had been trapped. We placed the young hares in a litter site created at the base of a willow, under a deadfall, or at the base of a cluster of trees, so that the female could easily find them. Before placing the young at this site we held them up to the female, who was in a Tomahawk trap. Once the litter was settled, the trap was opened and the female was allowed to leave when ready, often stepping up to or over the litter.

We pooled the data from all areas because we considered an individual hare 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 based on the proportion of reproductive females trapped within 1 week of the mean parturition date for each litter group. We also used necropsy studies to obtain additional data on litter size and parturition date (estimated from prenatal hare size as per Bookhout 1964 and Dell and Schierbaum 1974). Gestation periods for litters 2 and 3 were determined using 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 dependence between the birth masses of littermates, we used mean birth mass and mean right hind foot length for each litter in the analyses. Only masses 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. Stillbirth rates were determined by calculating the proportion of stillborn young to total young born, excluding newborn hares that were dead but for which the cause of death could not be confirmed.

To obtain a density estimate for each year, we averaged the spring density estimates provided by the Kluane Project (average of the program CAPTURE (Otis et al. 1978) and the Jolly–Seber method (Seber 1982)) for the three control grids to provide an estimate for the entire valley.

Age of females was calculated from the age at first capture starting in 1986 (Hodges et al. 1999). All animals were ear-tagged 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 an age of 1. Animals caught as juveniles during the summer or fall were assigned "known" ages and 1 year was added to each age class on January 1. Minimum-age and known-age categories for each year were pooled to arrive at the age distribution across the cycle. We used these assigned ages to group individual female hares into two categories, "yearling" and "2 years old and older".

Total reproductive output per female each year was estimated by multiplying the mean litter size by the pregnancy rate for all litter groups. Stillbirth rates were not used when calculating reproductive-output results so that direct comparisons with "potential natality" in Cary and Keith (1979) could be made. However, stillbirth rates can impact natality, as was observed during the first year of the decline (1991).

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

Results

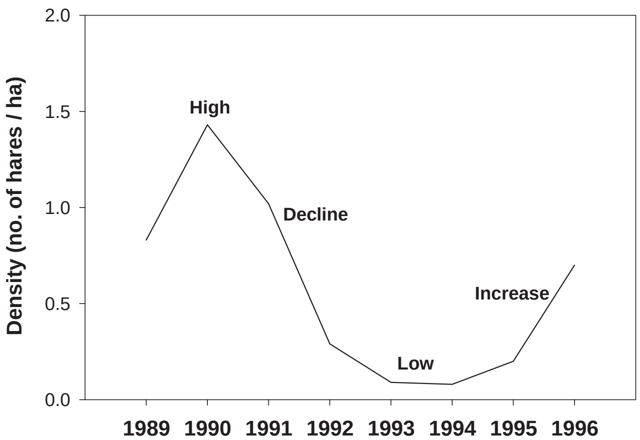
Snowshoe hare density

The density estimates for this snowshoe hare population are provided in Fig. 1. Hare densities were highest in 1990, declined through 1993, remained low through 1994, and began increasing again in 1995.

Parturition dates and gestation periods

Timing of the first litter varied significantly across years ($F_{[57]} = 25.36$, $p < 0.001$), but occurred in the third week of May in 4 of the 7 years examined (Table 1). The mean birth date was approximately 1 week later in 1991 and 1992 and nearly 2 weeks earlier in 1994. The mean gestation period for individual females caught during successive gestation

Fig. 1. Density of snowshoe hares (*Lepus americanus*) in the Yukon population during different phases of the cycle.



periods (36–38.5 days) fell within the range reported for snowshoe hares (36–40 days; Severaid 1942).

Pregnancy rates

Pregnancy rates (Table 2) varied significantly among years ($\chi^2_{[6]} = 57.38$, $p < 0.001$) and litter groups ($\chi^2_{[2]} = 25.23$, $p < 0.001$). All females trapped in 1994 through 1996 were pregnant. Although we trapped hares pregnant with a fourth litter in 1994 and 1995, pregnancy rates and litter characteristics were not measured. 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.

Stillbirth rates

Few young were stillborn, with rates exceeding 10% for only two litter groups (Table 3). Stillbirth rates varied significantly among years ($\chi^2_{[6]} = 24.72$, $p < 0.001$), but not by litter group ($\chi^2_{[2]} = 4.10$, $p = 0.13$). Few stillbirths occurred in litter 1 (0% in 5 of 7 years), but increased to an average of approximately 7% in later litter groups. The highest stillbirth rate (30.4%) occurred in the second litter of 1991, the first year of the decline.

Litter sizes

Age of the mother had no effect on litter size ($F_{[1]} = 0.34$, $p = 0.56$), so age classes were pooled. There was significant variation in mean litter size among years (range 3.8–5.5; $F_{[6]} = 2.78$, $p < 0.02$) and among litter groups (range 3.6–5.8; $F_{[2]} = 39.59$, $p < 0.001$), and a significant interaction between year and litter group ($F_{[10]} = 3.48$, $p < 0.001$; Fig. 2). The mean size of the first litter (3.6 ± 0.12; mean ± SE) did not vary among years, but was consistently smaller than the average litter sizes for litter 2 (5.8 ± 0.17) and litter 3 (5.3 ± 0.23).

Reproductive output

Total reproductive output varied by year (Fig. 3*a*), declining sharply from 12.8 young per female at peak hare densities in 1990 to low values of 6.9 (1991) and 7.0 (1992) during the decline. In the second year of the low (1994) and early increase (1995) phases, snowshoe hares were producing an estimated maximum of 18.9 young per female. For these 2 years, when the fourth litter was not measured, we estimated the total reproductive output by adding 3 young per female to the reproductive output from the first three litters. This addition represented a mean litter size of 4 × 85% pregnancy rate, a conservative estimate based on last-litter sizes from other years. Although litters remained larger than average in 1996, female hares did not produce a fourth litter, which resulted in a decrease in reproductive output to 15.5 young per female in the second year of the increase phase of the cycle.

Neonate measurements

Sex ratios did not differ significantly from 1:1 for any litter group ($\chi^2_{[2]} = 2.69$, $p = 0.26$) or year ($\chi^2_{[6]} = 11.40$, $p = 0.08$), so the data were pooled. Mean birth mass varied significantly with year ($F_{[6]} = 9.67$, $p < 0.001$), litter group ($F_{[2]} = 21.16$, $p < 0.001$), and age of the mother ($F_{[1]} = 8.79$, $p < 0.005$), but there was no interaction between year and litter group ($F_{[10]} = 1.62$, $p = 0.10$; Fig. 4*a*). Newborns in 1990 (peak), 1995, and 1996 (increase) were 10–20 g heavier than in 1991 (decline) and birth masses increased from the decline through the increase phase. Mean birth masses of litters 1 and 2 did not differ from each other, but were 5–20 g less than birth masses of litter 3. Yearling females had slightly smaller young (61.8 ± 0.98 g; mean ± SE) than older females (66.1 ± 2.72 g). Of the 6 years where both age classes were represented, this trend appeared in 4.

The age of the mother had no effect on offspring skeletal size measured as right hind foot length ($F_{[1]} = 1.39$, $p = 0.24$), so the age classes of females were pooled. Mean right hind foot length of newborn hares varied significantly with year ($F_{[6]} = 6.89$, $p < 0.001$) and litter group ($F_{[2]} = 16.68$, $p < 0.001$), but there was no interaction between year and litter group ($F_{[10]} = 1.33$, $p = 0.21$; Fig. 4*b*). For young hares born in 1991 (early decline), the right hind foot was shorter than in any other year except 1992, and longer for those born in 1996 (increase) than those born during the peak (1989 and 1990) and early decline (1991). Sample sizes were not large enough in 1992 to detect statistical differences. Litters 1 and 2 did not differ in mean right hind foot length, but hares born in these litters had shorter hind feet than those born in litter 3.

There was a significant positive relationship between right hind foot length and birth mass for newborn hares ($r^2 = 0.73$, $p < 0.05$). When right hind foot length was used as a covariate in an analysis of covariance comparing mean birth masses, the slopes of the regression lines differed significantly among litter groups and among years. These results suggest that some groups were heavier or lighter for a given right hind foot length. To determine in which years and litter groups these differences occurred we compared the residuals of birth mass from the regression in a two-way analysis of variance. Residuals of birth mass varied significantly across years ($F_{[6]} = 5.91$, $p < 0.001$), among litter groups ($F_{[2]} = 4.74$, $p < 0.01$), and in the interaction between year and litter group ($F_{[10]} = 3.01$, $p < 0.002$; Fig. 5). Hares born during 1990 (peak) and 1996 (increase) were heavier than average for a

Table 1. Parturition dates and gestation periods for snowshoe hares (*Lepus americanus*) in different litter groups for each year.

Year	Litter group	Parturition date: Mean	SE (days)	Range	*n*	Gestation period (days)	*n*
1989	1	25 May	0.7	23 May – 29 May	8	—	—
	2	2 July	0.9	26 June – 7 July	13	36.0	1
	3	7 August	1.3	2 August – 13 August	7	38.5	2
1990	1	24 May	0.6	20 May – 29 May	14	—	—
	2	26 June	0.7	21 June – 5 July	27	37.0	5
	3	31 July	0.4	28 July – 5 August	19	37.6	8
1991	1	29 May[a]	1.1	27 May – 3 June	7	—	—
	2	6 July	0.7	2 July – 9 July	11	38	3
	3	—	—	—	0	—	
1992	1	31 May[b]	3.0	29 May – 11 June	6	—	—
	2	6 July	4.5	26 June – 11 July	2	—	0
	3	—	—	—	0	—	—
1994	1	12 May[c]	0.8	9 May – 17 May	11	—	—
	2	18 June	1.0	14 June – 24 June	9	38.5	2
	3	25 July	1.2	20 July – 2 August	10	37.6	7
1995	1	22 May	2.4	16 May – 2 June	6	—	—
	2	20 June	1.3	13 June – 27 June	9	37.0	2
	3	28 July	1.4	28 July – 2 August	8	37.6	7
1996	1	22 May	0.7	19 May – 28 May	12	—	—
	2	27 June	0.9	22 June – 4 July	14	37.5	2
	3	2 August	0.6	30 July – 5 August	13	36.4	10

Note: Parturition dates are based on the number of pregnant hares that were caged and subsequently gave birth. Gestation periods are based on pregnant hares caught for successive litters.

[a]Significantly later than 1994–1996; $p < 0.05$.

[b]Significantly later than 1990, 1994–1996; $p < 0.05$.

[c]Significantly earlier than all other years; $p < 0.001$.

Table 2. Pregnancy rates (%) for litter groups by year.

	1989	1990	1991	1992	1994	1995	1996
Litter 1	90.9 (32)	89.4 (67)	100 (7)	77 (9)	100 (14)	100 (17)	100 (29)
Litter 2	96.8 (31)	96.2 (52)	85 (13)	100 (9)	100 (8)	100 (17)	100 (21)
Litter 3	82.4 (34)	86.4 (50)	0 (13)	0 (7[a])	100 (8)	100 (12)	100 (27)
Litter 4	—	—	—	—	na	na	—

Note: For each litter group the pregnancy rate was calculated as the percentage of all females trapped within 1 week of the mean parturition date (numbers in parentheses) that were reproductive. Pregnancy rates were not measured for the fourth litter in 1994 and 1995.

[a]As trapping records were not available for the second litter in 1992, the sample size used for this analysis was obtained by estimating the number of female hares based on previous trapping success in 1992 and factoring in adult mortality.

Table 3. Stillbirth rates (percentage that were stillborn) for litter groups by year.

	1989	1990	1991	1992	1994	1995	1996
Litter 1	0 (29)	7.3 (55)	0 (20)	0 (13)	3.1 (32)	0 (17)	0 (40)
Litter 2	7.7 (78)	4.5 (156)	30.4 (46)	0 (6)	0 (48)	1.6 (62)	6.3 (80)
Litter 3	6.3 (32)	13.6 (81)	—	—	4.7 (64)	8.9 (45)	1.3 (79)

Note: Stillbirth rates were calculated from the percentage of hares confirmed to be stillborn, based on necropsies of dead newborn hares. Numbers in parentheses show the total sample size.

given right hind foot length. Hares born in all other years were lighter than average, with the lightest hares born in 1992 (late decline), and were heavier through the increase. In 5 of the 7 years, the birth mass of neonates relative to their skeletal size was essentially consistent among litter groups; however, the mass to size relationship of neonates was disparate among litter groups for 1989 and 1991, when birth mass increased throughout the breeding season.

Fig. 2. Litter sizes (mean ± SE) of snowshoe hares in litters 1 (●), 2 (▽), and 3 (■) for all years. Population changes are indicated by density estimates (—).

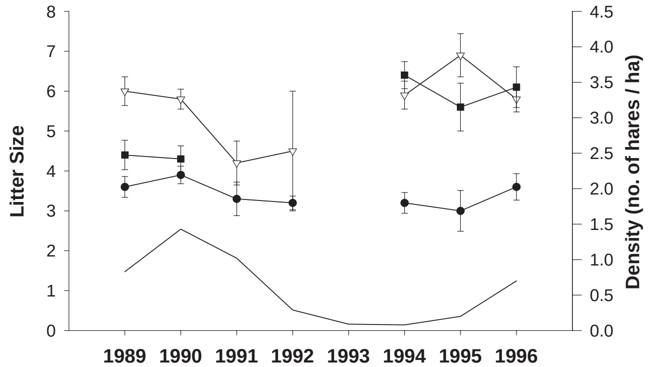


Fig. 3. Reproductive output (●) and population changes (—) for snowshoe hares during the same phases of the cycle in the Yukon (*a*) and Alberta (*b*). Pregnancy rates and litter sizes for litter 4 in 1994 and 1995 in the Yukon were estimated on the basis of last-litter sizes from other years and added to the total for the first three litters (○). The peak phases are vertically aligned between locations (Yukon, 1990; Alberta, 1971) for ease of interpretation. Data for Alberta are modified from Cary and Keith (1979).

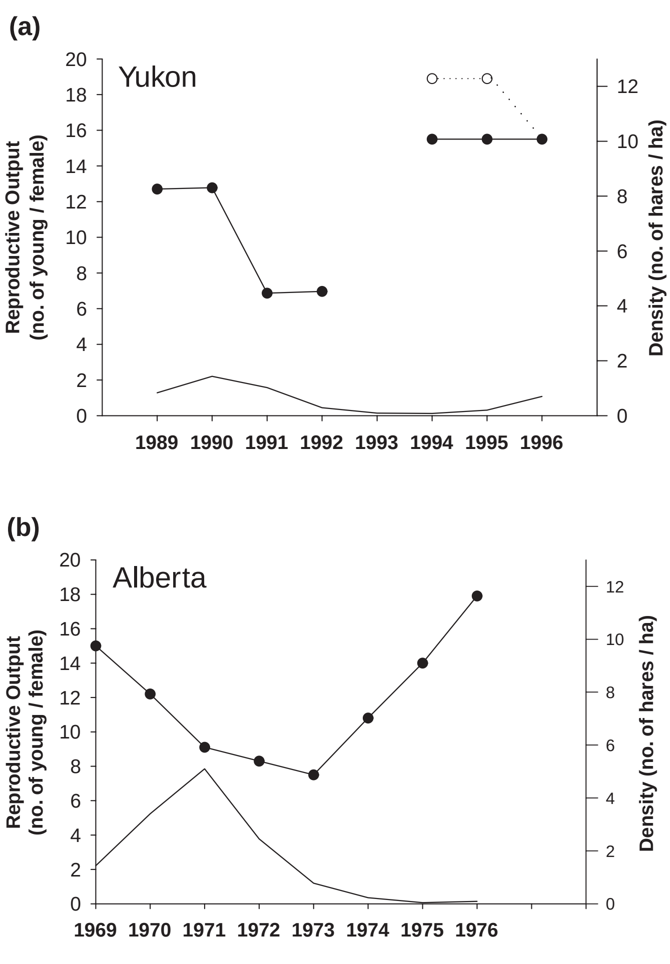


Fig. 4. Birth masses (*a*) and right hind foot lengths (*b*) (mean ± SE) of newborn snowshoe hares in litters 1 (●), 2 (▽), and 3 (■) for all years. Population changes are indicated by density estimates (—).

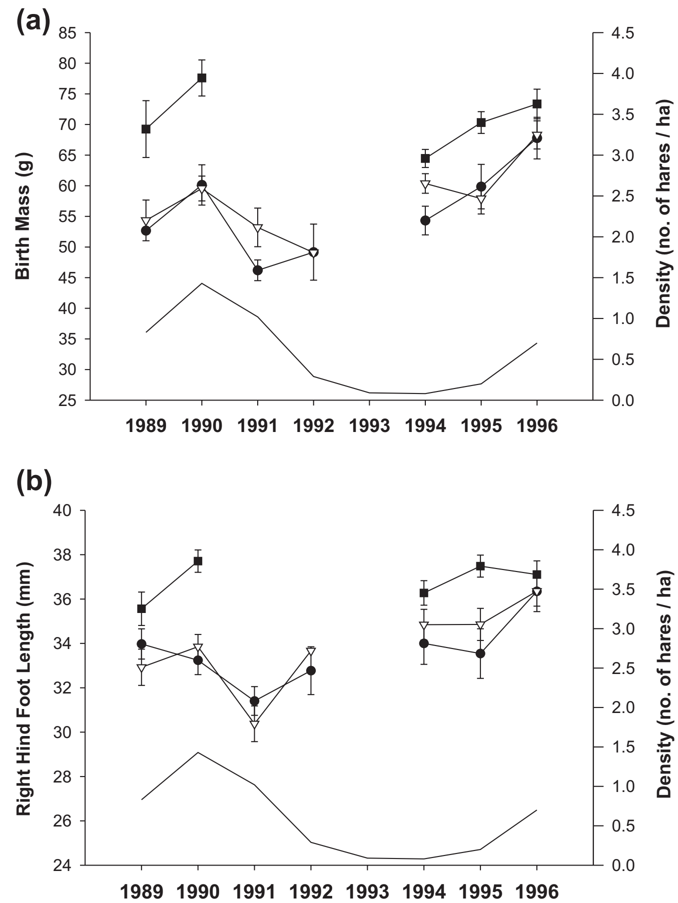
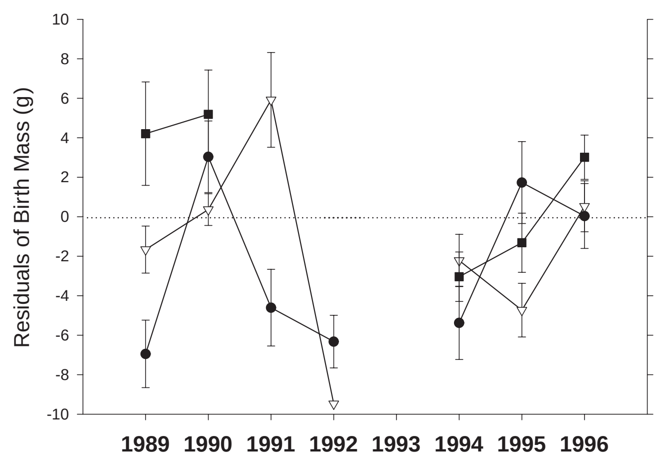


Fig. 5. Residuals of birth mass (mean ± SE) for newborn snowshoe hares in litters 1 (●), 2 (▽), and 3 (■) for all years. Population changes are indicated by density estimates (—).



Discussion

Reproduction across the cycle

All 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 phase and highest in the late low and early increase phases. These trends were similar to those reported by Cary and Keith (1979); however, litter sizes and the average number of litter groups produced during the breeding season differed between the two populations. In each breeding season, snowshoe hares in the Yukon population typically produced three litters ranging in size from 3.5 to 5.7 young per litter compared with four litters ranging from 2.6 to 4.9 young per litter for the Alberta population (Cary and Keith 1979). The differences in litter size and number of litter groups per breeding season were consistent with the results of other studies carried out at 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 at central latitudes (Alberta) and increasing litter size from south to north (Wisconsin to Alaska). Many of the studies used in Keith et al. (1966) spanned only 1–3 years and, as the number of litters and litter size vary with the cycle (Table 1, Fig. 2), the extent of latitudinal differences would be clearer if the phase of the cycle were known. From the information known at the time, Keith et al. (1966) suggested that 2 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 during 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; nonhibernating rodents and lagomorphs, Lord 1960; cottontail rabbits, Barkalow 1962).

Despite the differences in number of litter groups and litter size, changes in reproductive output across the cycle were similar for the Yukon (range 6.9–18.9) and Alberta (range 7.5–17.8; Fig. 3). One difference between the two populations is that fecundity remained high during the peak in the Yukon, whereas it had decreased by 32% in Alberta. Since each study examined one cycle, more data are needed to determine which result is more common. The amplitude and rate of change in reproduction appear to vary with the cycle, even in the same location, and may be associated with 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 phase and highest values early in the increase phase. 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 study (Hewson 1976).

Changes in reproductive output in this study were due primarily to changes in pregnancy rate and litter size in later litter groups, as in Alberta (Cary and Keith 1979). Both studies described first a decrease in pregnancy rate and litter size 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 the 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 suggested (Cary and Keith 1979) that the condition of the females fluctuated with the phase of the cycle. Studies of reproduction in other small-mammal populations have also reported similar fluctuations in litter size with population. 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 a cyclic *M. montanus* population, the change in litter size consistently preceded the change in density by 1 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. 1999), the proportion of yearling females in the population parelleling cyclic changes in reproductive output. As reproductive output was a function of litter size and pregnancy rate and no differences in litter size between yearling and older females were found, it is not surprising that reproductive output also did not differ. The lack of difference in litter size between age classes was supported by Cary and Keith (1979), who used an eye-lens mass – 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 for the Alberta hare population (Cary and Keith 1979) and mountain hares in Scotland (Hewson 1976).

In this study, the only significant effect of maternal age was on mean birth mass of neonates. In some years, young born to yearling females were up to 4 g lighter than those born to older females. However, the differences in birth mass were potentially biased by unequal sample sizes of both age classes of mothers among years and litter groups. As birth mass 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 not known whether females born later in the summer were at a disadvantage in the following 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 study did not differ between litter groups (O'Donoghue and Krebs 1992), a trend toward smaller skeletal sizes of hares during the decline (Hodges et al. 1999) may have been 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 phase.

A number of studies have described either an increase in reproductive success with age (e.g., Monson and DeGange

1995; Sand 1996) or a parabolic relationship where success first increases and then decreases in later years (Weimerskirch 1992). As female snowshoe hares breed as yearlings, unlike many longer lived animals, the effect of age on reproduction 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 (*Lepus europaeus*), particularly early in the breeding season (Lloyd 1968; Iason 1990). It was not possible to detect small differences, as sample sizes of "known"-age animals from particular litter groups were low and varied among years.

Neonate measurements

The variation in birth mass and right hind foot length of young hares also fluctuated with the cycle phase and followed a similar pattern of change to reproductive parameters. The smallest litters, shortest right hind feet, and lightest birth masses occurred during the decline phase (1991 and 1992). During the increase phase (1995 and 1996), litter size and birth mass remained high for litters 2 and 3, suggesting that females were in good condition through the entire breeding season. In addition, during the late low and early increase phases (1994 and 1995), hares produced a fourth litter. This pattern was in contrast to the high phase (1989 and 1990), where birth masses remained high for litter 3 but litter size decreased significantly. An analysis of changes in body condition of hares based on a mass – skeletal size regression suggested that during the decline phase, adult females were proportionately larger than during the increase and high phases of the cycle (Hodges et al. 1999). As reproductive output was lowest during the decline, this result suggested that females were not compromising their own mass for reproductive output during this period. Therefore, other measures of maternal condition should be investigated to determine the physiological link to changes in reproduction.

Because of the difficulty of trapping pregnant hares during the low phase (1992), sample sizes were small and this decreased the power to detect statistical differences between this and other years. Our data were not sufficient to determine whether the trend toward smaller litters and smaller neonates continued through the low phase or began to increase while populations were at low density.

The linear relationship between birth mass and right hind foot length for newborn hares differs markedly from the curvilinear relationship seen in adult hares (O'Donoghue and Krebs 1992). Adult hares weigh proportionately more with increasing right hind foot size. Although there was some variability in birth mass for a given right hind foot length among years and litter groups, hares in the third litter (in years when there was a third litter) were proportionately heavier than those in the first two litters. These results suggest that adult females were still in good condition in midsummer, likely because of 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 hares born during decline years. In a related study, neonate size was correlated with the preweaning juvenile survival rate (Stefan 1998). Hares born during the increase phase had higher survival rates than hares born during the decline.

Conclusion

Snowshoe hares are capable of having four litters in a breeding season, yet fail to do so even when food is apparently abundant and predator numbers are relatively low. Owing to changes in both pregnancy rate and litter size, reproductive output in this snowshoe hare population was lowest during the decline phase, highest during the late low and early increase phases, and declined at peak hare densities. Neonate measurements followed a similar trend; however, newborn hares continued to get bigger during the increase phase, reaching a maximum size and mass 1 year after the peak in reproductive output. The similarity between the Yukon and Alberta populations in the fluctuation of reproductive measures suggests that these patterns are repeatable and widespread.

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