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Effects of supplemental food on snowshoe hare reproduction and juvenile growth at a cyclic population peak

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Summary

1. Snowshoe hare (*Lepus americanus* (Erxleben)) populations were provided with supplemental food on two study grids in the south-west Yukon to examine the effects of food on reproduction and juvenile growth.
2. Timing of parturition, pregnancy rates, litter sizes, male breeding condition, and juvenile growth rates were measured on two food grids and on two control grids during two summers at a cyclic peak in hare numbers.
3. Most female hares gave birth to three litters per summer, and parturition was in approximate synchrony, such that there were three distinct litter groups per season.
4. The main effects of food addition were to increase hare densities 2·1- to 2·7-fold, advance the timing of breeding by about 1 week in 1 year, and increase pregnancy rates by 5% relative to the controls.
5. There were no significant differences in litter sizes, lengths of male breeding seasons, juvenile growth rates, or total female reproductive output between hares on the food and control grids.
6. Third litter stillborn rates were higher, and third litter juvenile growth rates slightly lower on food grids relative to those on controls, possibly reflecting an effect of higher densities.
7. This study suggests that food is not a proximate factor limiting hare reproduction and early juvenile growth at the observed peak hare densities.

Key-words: snowshoe hare, food addition, reproduction, growth and population cycle.

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Introduction

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

While food addition can affect the density and many demographic characteristics (e.g. pregnancy rates, litter sizes, survival rates) of animal populations, it generally has not altered patterns of population change (Boutin 1990). In particular, the addition of food has not prevented major population declines of many small mammal species that undergo periodic cyclic fluctuations in numbers (e.g. Krebs & DeLong 1966; Cole & Batzli 1978; Ford & Pitelka 1984; Krebs *et al.* 1986).

Snowshoe hare populations fluctuate widely in a '10-year' cycle, more or less synchronous throughout

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

While overwinter juvenile mortality was the demographic parameter most closely associated with the rate of population change in Keith's studies (Keith & Windberg 1978), major changes in reproductive output (i.e. pregnancy rates, ovulation rates, litter sizes and breeding season length) were also closely associated with the cycle in population density. Cary & Keith (1979) presented a detailed analysis of reproductive change in the hare cycle and concluded that most reproductive parameters cycled in synchrony, resulting in a 2·4-fold increase in potential natality from the low to the peak in the reproductive cycle. The peak in reproduction preceded the population density peak by about 3 years, and at maximum hare densities, reproductive output had already declined considerably. Cary & Keith (1979) attributed this to the effect of food shortage at peak densities. In the Yukon study, reproductive parameters were not directly measured, but an index of recruitment (number of juveniles trapped per adult female) was highly correlated with the rates of population change (Krebs *et al*. 1986).

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

Methods

The study area was located in the Kluane Lake region of south-west Yukon Territory, Canada (61°N, 138°W). The dominant vegetation of the area was white spruce forest (*Picea glauca* Blake), with a dense but patchy shrub understorey of mostly willow (*Salix glauca* L. and *S. alaxensis* (Andess). Cov.), soapberry (*Shepherdia canadensis* (L.) Nutt) and bog birth (*Betula glandulosa* Raup.) (Douglas 1974).

Hare trapping

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

Eight-six live Tomahawk traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin) were placed on each grid at stations 30 m apart. We trapped hares on all four grids for at least 2 days every other week from May to September 1989 and 1990. On several occasions disturbance of the traps by bears caused postponement of trapping sessions. Upon capture, each hare was weighed with a spring scale, its right hind foot was measured as an index of body size, and a monel ear tag (No. 3, National Band and Tag Co., Newport, Kentucky, USA) was placed in its right ear. The reproductive condition of males was noted as scrotal, testes receding, or abdominal, based on testes size and position. We distinguished between pregnant and non-pregnant females only in the week before birth, when the increased body size of pregnant females was apparent. Females were also classified as lactating–nursing, lactating–not nursing, and not lactating (according to criteria given in Keith, Meslow & Rongstad 1968).

Measurement of litters

Snowshoe hares do not have burrows or make nests (Severaid 1942; Graf & Sinclair 1987), and thus their litters are very difficult to locate in the field. In order to estimate litter sizes, we trapped pregnant females shortly before parturition, and placed them in 60 × 60 × 120 cm chicken wire cages covered with burlap and provided with ample spruce branches and grass for natural cover within. These cages met standards established by the Canadian Council on Animal Care (1984), and the captive hares were fed commercial rabbit chow, natural forage, and apples *ad libitum*. On control grids, the cages were placed within each female's home range, adjacent to her capture site. However, due to disturbance of cages by bears on the food grids, all cages were placed within small (0·55–1·0 ha) enclosures surrounded by electric fences. We transported pregnant females to and from these 'nurseries' upon capture and after parturition. Female hares spent a mean of 6·2 days in these cages before giving birth to their litters.

Upon parturition, female hares were immediately released. On the control grids, females were simply let out of their cages, while on the food grids they were carried with their litters back to their home ranges. We counted each hare litter, and weighed, measured (right hind foot length), sexed, and ear-tagged (No.1 monel tags) the individual leverets. On two of the grids (Food1, Control1), we also affixed 2-g radio transmitters (Models SR-1 and SR-2, Biotrack, Dorset, UK) with glue to the backs of half of the juveniles in each litter to look at subsequent survival. We attempted to recapture all radioed leverets after approximately 10 days to measure growth rates and re-glue radios.

Determination of reproductive parameters

As male snowshoe hares become scrotal during the late winter (Cary & Keith 1979; Boutin 1984a), we were unable to determine the timing of onset of breeding condition in males because we started trapping each year in May. We did, however, record the chronology of testes regression in late summer from trapping data. The mean dates of parturition of caged hares were calculated as measures of the timing of breeding on each of the study grids. Over the course of the study, seven out of 201 pregnant females died in cages or traps, and we autopsied these to gain additional data on litter sizes and timing of parturition. We determined the age of hare embryos based on published chronologies of snowshoe hare prenatal development (Bookhout 1964; Dell & Schierbaum 1974).

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

Pregnancy rates per litter group were estimated from the proportion of trapped females obviously pregnant, or having just given birth during a period of 1 week either side of the mean parturition date for the grid. We used litter sizes from caged and autopsied females as measures of mean natality per litter group.

Statistical procedures

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

We calculated indices of spring condition for adult males from May trapping data, using the relationship between body weight and right hind foot length, as in Bailey (1968). A power curve was fitted to the weight and foot length measurement (using the NONLIN module, SYSTAT, Inc., Evanston, Illinois, USA) from all Kluane Project May trapping data from males on the control grids in 1989 and 1990. The resulting relationship, $WT(\mathrm{g}) = 738{\cdot}9 + RHF(\mathrm{mm})^{1{\cdot}3}$, was used to calculate a predicted weight for a hare with a given right hind foot length. The condition index for that hare was then calculated as observed weight/predicted weight. Condition indices were calculated for males only, as most females were pregnant when May trapping commenced, and their weights were influenced by their gestation stage.

Gompertz growth curves were fitted to the observed body weights of trapped and radioed juvenile hares (sex combined) according to the methods of Kaufmann (1981). In preliminary analyses, Gompertz growth curves fit the hare growth data better than logistic or Bertalanffy curves. Growth rates were thus measured as 'specific growth rates', or the percentage increase in size per day. We compared growth rates using analysis of covariance, with age as the covariate, and included only one randomly chosen point per animal in the analysis to maintain independence of the data.

We used factorial ANOVAS to investigate the influences of the food addition, year, litter group, and their interactions on hare body weights, condition indices, parturition dates, litter sizes, and juvenile birth weights (MGLH module, SYSTAT). Hierarchical log-linear models were used to analyse the effects of the same factors on pregnancy rates, stillborn rates, and sex ratios (TABLES module, SYSTAT). All other statistical tests were performed according to procedures in Zar (1984).

Results

Population density

Population sizes of hares on the food grids were, on average, double those on the control grids during the summers of both years (Table 1). These differences were statistically significant in two of the four time periods considered (*t*-tests; May 1989, $t = 8{\cdot}22$, df = 2, $P = 0{\cdot}03$; August 1990, $t = 8{\cdot}22$, df = 2, $P = 0{\cdot}01$). Population sizes were similar between the 2 years of study.

Spring body weights and condition indices

Body weights and condition indices of adult male hares in spring indicated the same differences between animals on the food and control grids (Tables 2 & 3). Males on the food grids were about 10% heavier and in better body condition than those on controls in May 1990, but not in May 1989. The year and year × treatment effects were statistically significant for both parameters, but the food treatment effect was not at $P = 0{\cdot}05$.

Timing of testicular regression

All adult males were scrotal on all four grids in both years at the start of trapping in May. Testicular regression was first apparent in the second half of July on both food and control grids (Food, 73·3% scrotal; Control, 60·4% scrotal), by mid-August fewer than half of the males were fully scrotal (Food, 31·6%; Control, 35·3%), and by late August all males were abdominal or had receding testes. Therefore, food addition had no apparent effect on the cessation of breeding in males.

Table 1. Jolly-Seber population estimates (±SE) of snowshoe hares on the four study grids in 1989 and 1990

Trapping period	Population estimates (hares per grid)			
	Food1	Food2	Control1	Control2
May 1989*	122 ± 43	102 ± 48	33 ± 5	49 ± 3
Aug 1989	128 ± 17	194 ± 42	123 ± 18	67 ± 8
May 1990	148 ± 32	84 ± 19	64 ± 5	44 ± 9
Aug 1990*	184 ± 32	187 ± 51	107 ± 22	124 ± 36

* Significant difference between food and control grids, $P < 0{\cdot}05$.

Table 2. Body weights (±SD) of male snowshoe hares in spring on study grids (sample sizes in parentheses)

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

Factorial ANOVA	*F*-value	df	*P*
Main effects			
Treatment	6·38	1,2	0·13
Year	44·85	1,2	0·02*
Two-way interactions			
Treatment × Year	57·26	1,2	0·02*

Pregnancy rates

Most female hares on the study grids had three litters during the summers of 1989 and 1990 (Table 4). Pregnancy rates were high in all periods, but were higher on food grids (95·4%) than on controls (90·6%), and also varied with litter group (litter 1 = 94·5%, litter 2 = 97·7%, litter 3 = 88·5%).

Timing of litters

The mean dates of parturition were advanced by approximately 1 week on the food grids in 1989, and by 3–4 days in 1990, relative to those on the controls (Table 5). Both the treatment and year × litter effects on birth dates were statistically significant. The significant interaction effect reflected earlier third litters on all grids in 1990, while the first and second litters were born at about the same time each year, particularly on the food grids.

Evidence of superfoetation

The European hare (*Lepus europaeus* Pallas) is able to shorten the interval between successive litters by successfully mating during a pre-partum oestrus several days before the birth of a litter in gestation (Martinet, Legouis & Moret 1970). In this way, the female can be pregnant with two litters, each

Table 3. Condition indices (observed weight/predicted weight ± SD) of male snowshoe hares in spring on study grids (sample sizes in parentheses)

Year	Condition indices			
	Food1	Food2	Control1	Control2
1989	1·034 ± 0·098 (43)	1·014 ± 0·082 (12)	0·992 ± 0·098 (16)	1·007 ± 0·082 (27)
1990	1·098 ± 0·091 (53)	1·075 ± 0·135 (22)	0·977 ± 0·100 (34)	1·017 ± 0·087 (14)

Factorial ANOVA	*F*-value	df	*P*
Main effects			
Treatment	10·71	1,2	0·08
Year	25·42	1,2	0·04*
Two-way interactions			
Treatment × Year	29·69	1,2	0·03*

Table 4. Pregnancy rates adult female hares on study grids (sample sizes in parentheses)

		Pregnancy rates (%)			
Year	Litter	Food1	Food2	Control1	Control2
1989	1	92·9 (42)	90·3 (31)	100·0 (11)	90·5 (21)
	2	100·0 (21)	100·0 (46)	94·1 (17)	100·0 (14)
	3	95·5 (22)	97·2 (36)	82·4 (17)	82·4 (17)
1990	1	100·0 (80)	97·4 (39)	91·7 (36)	87·1 (31)
	2	96·8 (31)	97·2 (36)	96·6 (29)	95·7 (23)
	3	73·1 (26)	94·1 (51)	81·5 (27)	91·3 (23)

Log-linear models	*G*-value	df	*P*
Main effects			
Treatment	6·40	1	$0·01 < P < 0·025$*
Year	0·13	1	$0·50 < P < 0·75$
Litter	15·89	2	$P < 0·001$***
Two-way interactions			
Treatment × year	0·03	1	$0·75 < P < 0·90$
Treatment × litter	0·32	2	$0·50 < P < 0·75$
Year × litter	3·79	2	$0·10 < P < 0·25$

Table 5. Mean parturition dates (±SD in days) of hare litters born in cages on study grids (sample sizes in parentheses)

		Mean parturition date			
Year	Litter	Food1	Food2	Control1	Control2
1989	1	21 May ± 1·7 (8)	—	25 May ± 1·9 (8)	—
	2	22 Jun ± 2·4 (9)	25 Jun ± 1·8 (8)	2 Jul ± 3·5 (8)	4 Jul ± 2·9 (5)
	3	1 Aug ± 3·5 (9)	31 Jul ± 2·0 (7)	7 Aug ± 4·1 (5)	8 Aug ± 2·1 (2)
1990	1	19 May ± 2·5 (15)	22 May ± 1·5 (11)	26 May ± 1·4 (7)	24 May ± 2·8 (7)
	2	23 Jun ± 2·2 (11)	26 Jun ± 4·7 (16)	28 Jun ± 3·5 (14)	26 Jun ± 4·0 (13)
	3	29 Jul ± 2·4 (9)	25 Jul ± 2·8 (11)	1 Aug ± 1·9 (12)	30 Jul ± 1·4 (7)

Factorial ANOVA	*F*-value	df	*P*
Main effects			
Treatment	123·48	1,2	0·008**
Year	18·01	1,2	0·05
Litter	1516·67	2,4	<0·001***
Two-way interactions			
Treatment × year	6·37	1,2	0·13
Treatment × litter	0·19	2,4	0·84
Year × litter	2·03	2,4	0·04*

at different stages of development, at the same time ('superfoetation'). Flux (1981) suggested that this may occur in snowshoe hares as well. The gestation period of snowshoe hares in 36–37 days (Severaid 1942).

In our study, the intervals between litter groups, based on mean parturition dates, varied from 27·5 to 39·5 days on the study grids. The mean interval was 37·4 days for the 37 individual females for whic the date of birth was known. We found evidence suggesting intervals between litters of less than 35 days in only two cases. When trapped in July 1989, two females on the Control1 grid appeared to have recently given birth to third litters, less than 30 days after their second litters dropped. However, we could not find the nests of these two females to confirm that they did exhibit superfoetation. If it does occur, superfoetation does not appear to be a common phenomenon in snowshoe hares at Kluane. No evidence of superfoetation has been observed in a colony of captive snowshoe hares held at the University of British Columbia either (A.R.E. Sinclair, unpublished data).

Litter sizes

The food addition had no significant effect on hare litter sizes (Table 6). Litters were the largest in the second litter group, and smallest in the first litter group of the summer (Multiple contrasts, $L2 > L3 > L1$, $P < 0·001$).

Stillborn rates

A surprisingly large number of newly born hares were stillborn in the cages (Table 7), although almost all were fully formed and of the same weights as live littermates. Live-trapping data indicated that the caging of female hares had no measurable effect on the number of offspring reaching trappable age (3–4 weeks), so we do not believe that the high number of stillborn young was a result of cage-induced stress (M. O'Donoghue, unpublished data). We also found no evidence of female hares eating their stillborn young, so we believe we were accurately able to count them. Stillborn rates were fairly low

Table 6. Mean litter sizes (±SD) of hare litters born in cages on study grids (sample sizes in parentheses)

		Mean litter sizes			
Year	Litter	Food1	Food2	Control1	Control2
1989	1	3·8 ± 1·2 (9)	–	3·6 ± 0·7 (8)	–
	2	5·6 ± 1·7 (9)	7·1 ± 1·5 (9)	5·9 ± 1·6 (8)	6·2 ± 0·8 (5)
	3	4·6 ± 1·1 (9)	5·1 ± 2·0 (7)	4·2 ± 0·4 (5)	5·5 ± 0·7 (2)
1990	1	3·8 ± 0·7 (15)	3·5 ± 0·8 (11)	3·9 ± 0·9 (7)	4·0 ± 0·8 (7)
	2	5·5 ± 2·2 (11)	6·6 ± 0·8 (16)	5·7 ± 1·4 (14)	5·8 ± 1·2 (13)
	3	5·8 ± 1·2 (10)	5·5 ± 1·1 (13)	4·1 ± 1·6 (12)	4·6 ± 1·3 (7)

Factorial ANOVA	*F*-value	df	*P*
Main effects			
Treatment	1·35	1,2	0·37
Year	0·01	1,2	0·95
Litter	22·44	2,4	0·01**
Two-way interactions			
Treatment × year	0·18	1,2	0·71
Treatment × litter	0·48	2,4	0·65
Year × litter	1·68	2,4	0·30

Table 7. Stillborn rates (% of total young born dead) for hare litters born in cages on study grids (sample sizes in parentheses)

		Stillborn rates (%)			
Year	Litter	Food1	Food2	Control1	Control2
1989	1	3·6 (28)	–	0·0 (29)	–
	2	6·0 (50)	6·3 (64)	0·0 (47)	19·4 (31)
	3	43·9 (41)	45·2 (31)	4·8 (21)	9·1 (11)
1990	1	9·5 (52)	17·6 (34)	14·8 (27)	0·0 (28)
	2	1·6 (61)	17·6 (74)	2·5 (80)	9·2 (76)
	3	18·9 (53)	29·1 (66)	8·2 (49)	21·9 (32)

Log-linear models	*G*-value	df	*P*
Main effects			
Treatment	11·33	1	$P < 0\cdot001$***
Year	0·83	1	$0\cdot25 < P < 0\cdot50$
Litter	38·85	2	$P < 0\cdot001$***
Two-way interactions			
Treatment × year	0·24	1	$0\cdot75 < P < 0\cdot90$
Treatment × litter	5·92	2	$0\cdot05 < P < 0\cdot10$
Year × litter	8·24	2	$0\cdot01 < P < 0\cdot025$*

(0–18%) in the first and second litter groups, but were higher in third litters, especially on the food grids where stillborn rates approached 50% in 1989.

Total reproductive output

An estimate of total reproductive output per female surviving the breeding season was made by multiplying pregnancy rates by mean litter sizes and (1 − stillborn rates), and summing these over the three litter groups (Table 8). This corresponds to Keith's 'potential natality' (Cary & Keith 1979). There were no significant differences between the food and control grids in either year (*t*-tests; 1989, $t = 0\cdot10$, df = 2, $P = 0\cdot93$; 1990, $t = 1\cdot41$, df = 2, $P = 0\cdot29$).

Sex ratios

There were no significant differences in sex ratios among litter groups, between years, or between food and control grids (Table 9). Sex ratios of newly born leverets differed statistically from 1:1 in only one case out of 22 total litter groups on the four study grids, a rate not different from that expected by chance at $P = 0\cdot05$. These results therefore suggest that the sex ratio of hares born at peak numbers was even.

Body weights of newborn hares

There were no significant differences between the mean body weights of newly born hares on food grids

Table 8. Total estimated reproductive output[a] per surviving female on study grids

	Reproductive output (juveniles per female)			
Year	Food1	Food2	Control1	Control2
1989	11·1	14·1[b]	12·5	12·4[b]
1990	12·1	11·8	11·5	11·8

[a] Total reproductive output = (pregnancy rate)(mean litter size)(1 − stillborn rate), summed over three litter groups.

[b] Mean first litter size estimated from other food grid or control grid.

Table 9. Sex ratios of hare litters born in cages on study grids (proportion of females, number of juveniles in parentheses)

		Sex ratios			
Year	Litter	Food1	Food2	Control1	Control2
1989	1	0·50 (20)	–	0·43 (21)	–
	2	0·59 (29)	0·57 (47)	0·60 (47)	0·48 (31)
	3	0·67 (33)	0·60 (10)	0·55 (20)	0·45 (11)
1990	1	0·58 (52)	0·67 (33)	0·52 (23)	0·54 (24)
	2	0·43 (61)	0·47 (72)	0·51 (80)	0·63 (73)*
	3	0·40 (52)	0·54 (61)	0·41 (49)	0·50 (32)

Log-linear models	*G*-value	df	*P*
Main effects			
Treatment	0·00	1	$P < 0\cdot975$
Year	1·38	1	$0\cdot10 < P < 0\cdot25$
Litter	1·20	2	$0\cdot50 < P < 0\cdot75$
Two-way interactions			
Treatment × year	1·86	1	$0\cdot10 < P < 0\cdot25$
Treatment × litter	4·19	2	$0\cdot10 < P < 0\cdot25$
Year × litter	4·73	2	$0\cdot05 < P < 0\cdot10$

* Significantly different from 1:1, $P < 0\cdot05$.

and those on controls, nor were there any significant differences in total litter biomasses between treatments (Table 10). In general, body size of third litter juveniles was the largest, especially on the control grids, and the effect of litter group on birth weights was statistically significant (multiple contrasts, L1 = L2 ($P = 0{\cdot}29$) <L3 ($P = 0{\cdot}01$)). Mean body weight of the litters was significantly negatively correlated with litter size ($r = -0{\cdot}49$, $P < 0{\cdot}001$), a result not found by Severaid (1942), but noted for hares in general by Flux (1981).

Growth rates of juvenile hares

The growth rates of juvenile hares (sexes combined) were not significantly different between the food and control grids (Fig. 1; ANCOVA, $F = 0{\cdot}002$, df = 1,125, $P = 0{\cdot}96$), but the effect of litter group was statistically significant (ANCOVA, $F = 3{\cdot}74$, df = 2,125, $P = 0{\cdot}03$). The treatment × litter interaction was not significant ($F = 1{\cdot}64$, df = 2,125, $P = 0{\cdot}20$). The Gompertz growth curves for the first two litter groups were nearly identical for the experimental and control grids, although the food grids have higher asymptotic values (Fig. 1a, b). From birth to age 60 days, first litter leverets gained an average of 16·3 g and 16·0 g, and second litter juveniles 14·6 g and 14·1 g per day on the food and control grids, respectively. Growth was nearly linear for the first 2–3 months. There was a trend for growth to be slower on food grids for the third litter group (Fig. 1c), but data were lacking for third litter juveniles older than 35 days. The estimated growth rates to 60 days age on the food and control grids were 13·7 g and 16·6 g per day, respectively.

Table 10. Mean juvenile weights at birth (±SD) for hare litters born in cages on study grids (number of litters in parentheses)

		Mean juvenile weights (g)			
Year	Litter	Food1	Food2	Control1	Control2
1989	1	60·7 ± 8·8 (6)	–	53·6 ± 7·1 (8)	–
	2	60·0 ± 8·3 (9)	53·4 ± 13·1 (8)	54·4 ± 14·0 (8)	54·2 ± 5·3 (4)
	3	63·4 ± 7·5 (8)	65·0 ± 13·8 (4)	73·0 ± 12·7 (5)	60·0 ± 4·8 (2)
1990	1	68·1 ± 8·8 (13)	63·4 ± 7·8 (10)	57·7 ± 15·2 (6)	62·6 ± 6·4 (6)
	2	63·2 ± 7·7 (11)	54·3 ± 8·6 (9)	60·8 ± 11·7 (14)	58·1 ± 8·7 (12)
	3	67·6 ± 5·3 (9)	52·3 ± 9·5 (10)	79·4 ± 13·9 (11)	74·3 ± 8·3 (6)

Factorial ANOVA	*F*-value	df	*P*
Main effects			
Treatment	0·09	1,2	0·80
Year	3·26	1,2	0·21
Litter	13·66	2,4	0·02*
Two-way interactions			
Treatment × year	1·87	1,2	0·31
Treatment × litter	6·60	2,4	0·05
Year × litter	0·19	2,4	0·83

Juvenile breeding

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

Discussion

There results are consistent with the findings of many vertebrate food-addition experiments in several respects. First, population sizes on the food grids were approximately double those on the controls, as found in most such studies (Boutin 1990). Body weights of the supplemented adult animals were also generally higher, at least in 1990. Third, the timing of female reproduction was advanced on the food grids in 1989, as reported in many other studies (e.g. Hansen & Batzli 1979 with *Peromyscus leucopus* (Rafinesque); Vaughan & Keith 1981 with snowshoe hares; Taitt & Krebs 1983 with *Microtus townsendii* (Bachman)). The 'onset of spring' was earlier in 1990 than in 1989 (i.e. higher temperatures and earlier snow-melt), and this may have been the reason that female hares on the control grids were able to advance reproduction in 1990 to match the dates on food grids (Conaway & Wight 1962; Cary & Keith 1979). We did not measure the timing of testicular recrudescence in the winter, but there is evidence that males became scrotal 1–3 weeks earlier on the food grids at Kluane (Boutin 1984a; D.S. Hik, unpublished data). Finally, the slightly higher pregnancy rates on the food grids suggest that food did have some effect on hare reproduction, although pregnancy rates were high on all grids.

However, the most striking pattern in these results is that the food addition had little or no effect on most of the demographic parameters measured. The timing of male testes regression was not different between treatments, contrary to the experimental results of Windberg & Keith (1976). Litter sizes were not significantly increased by the food addition, as opposed to a positive response in other studies (e.g. Kirkpatrick & Kibbe 1971 with *Sylvilagus floridanus* (J.A. Allen); Cole & Batzli 1978 with *Microtus ochrogaster* (Wagner); Vaughan & Keith 1981; Dobson & Kjelgaard 1985 with *Spermophilus columbianus* (Ord)). Juvenile growth was essentially the same on the food and control grids, with a possible trend towards lower growth of third litter juveniles on food addition grids. In previous studies, growth increased with food addition (e.g. Cole

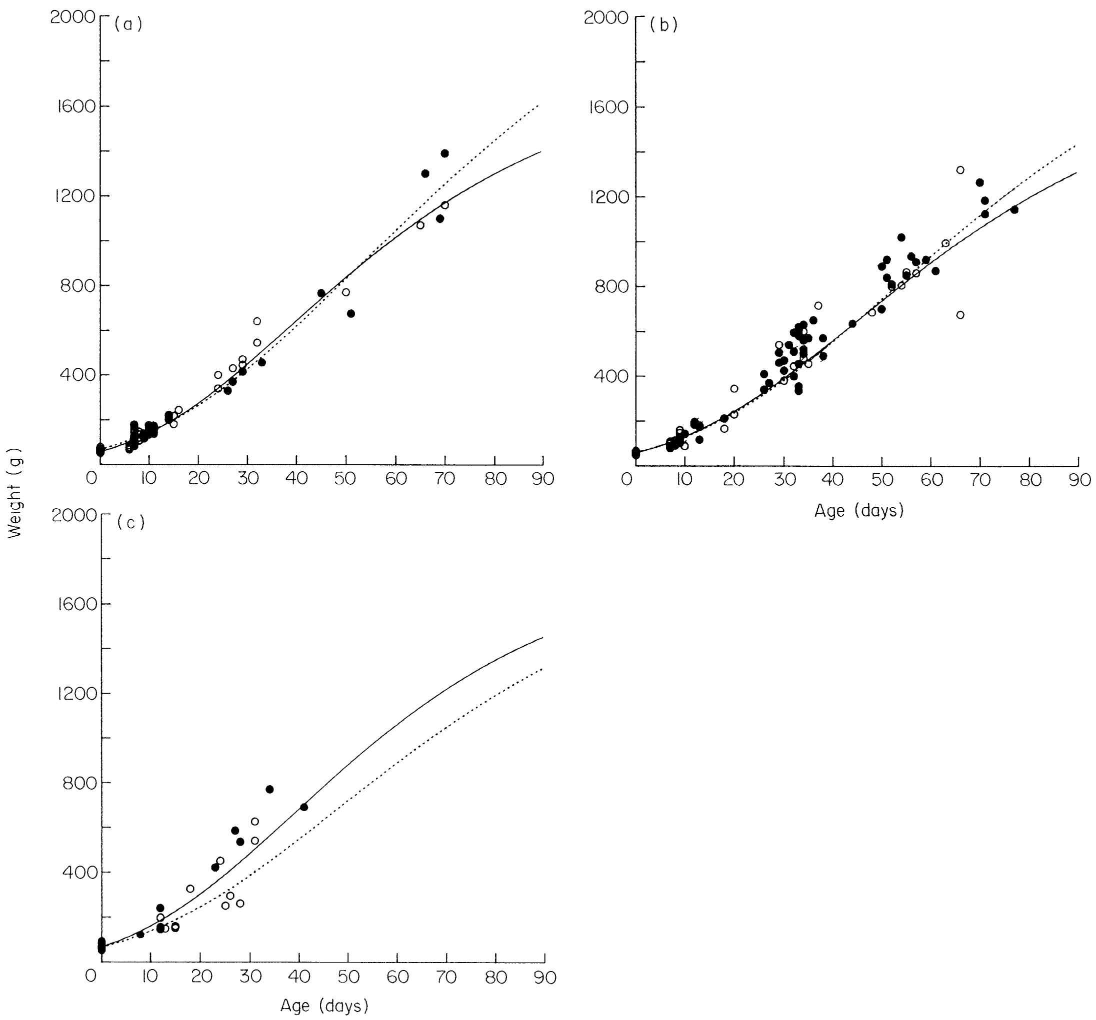

Fig. 1. Gompertz growth curves of (a) first litter (mean birth dates 19–26 May), (b) second litter (22 June–4 July), and (c) third litter (25 July–8 August) juvenile snowshoe hares on food (····○····) and control (—●—) grids in 1989 and 1990 (sexes combined). Only points from animals of known age are plotted, although the parameters for the growth curves were calculated from the measured growth of juveniles of unknown dates of birth as well.

& Batzli 1978; Vaughan & Keith 1981; Desy & Thompson 1983 with *Microtus pennsylvanicus* (Ord); Sullivan, Sullivan & Krebs 1983 with *Eutamias townsendii* Bachman). Most importantly, the overall reproductive output per female in our study was not greater in either year on the food grids.

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

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

2. *Food limited reproduction and growth on the controls and the food addition was adequate, but density-related factors other than food were limiting on the food grids.* Hare densities were 2–3 times higher on the food grids than those on the controls. These higher densities probably reflected the increased quality of the habitat on the food grids for hares, due to the food addition. According to habitat selection theory, animals should distribute themselves among habitats relative to their expected fitness in each habitat (Fretwell & Lucas 1970; Rosenzweig 1981). Thus, the most suitable habitats also have the highest animal densities. Fretwell & Lucas (1970) hypothesized that 'ideally' distributed animals will have the same mean expected fitness in all habitats, because the higher animal density in the best habitat decreases that habitat's suitability to the point where it is profitable (i.e. expected fitness would not be less) for animals to occupy more marginal habitat. Although reproductive output is only one component of inclusive fitness (see Morris 1989), we may have observed no differences in reproduction between the food and control grids due to adverse effects of factors related to the high density of hares on the food grids.

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

The effects of increased density on population dynamics of hares are little understood (Krebs 1986). There have been a number of hypotheses suggesting that behavioural changes in small mammals at high densities may cause population declines (Chitty 1960; Christian & Davis 1964). It is known that snowshoe hares form dominance hierarchies, and hares react aggressively towards subordinate conspecifics (Boutin 1984b; Graf 1985; Sinclair 1986). Whether or not increased stress due to social factors at high densities could affect the demography of hares is unknown. The high stillborn rates in the third litter on the food grids suggest that females on these grids were more physiologically stressed than those on the controls. The cause of these stillbirths is unknown, but the high physiological costs of nursing two previous litters (Hanwell & Peaker 1977; Kenagy 1987) could have combined with higher socially induced stress to contribute to the high rates of loss.

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

3. *Neither food nor density-related factors limited reproduction and juvenile growth at peak hare densities on the controls and food grids, so no response to food addition was observed.* Cary & Keith (1979) noted that peak hare reproduction occurred 3 years before the population peak, and was considerably lower at the highest hare density. They found correlations of most reproductive parameters with overwinter adult weight loss, and attributed the decline in reproduction to food shortage. This study found no important responses of hare reproduction and juvenile growth to food addition. The litter sizes and pregnancy rates that we observed on the control grids were higher than those recorded by Cary & Keith (1979) at peak densities in Alberta (although there is a general trend of increasing litter sizes from south to north in snowshoe hares; Keith, Rongstad & Meslow 1966). Likewise, the juvenile growth rates at Kluane ($13{\cdot}7-16{\cdot}6\,\mathrm{g\,day^{-1}}$) compared favourably to those recorded in the literature for captive hares with unlimited food ($14{\cdot}5\,\mathrm{g\,day^{-1}}$, Keith, Meslow & Rongstad 1968; $17{\cdot}1\,\mathrm{g\,day^{-1}}$, Graf & Sinclair 1987), and are higher than those presented by Vaughan & Keith (1981) for food-stressed leverets ($9{\cdot}8\,\mathrm{g\,day^{-1}}$). These observations suggest that although food may have been limiting to reproduction and juvenile growth in Keith's Alberta study area, it was not in the Yukon in 1989 and 1990 at the observed peak hare densities. It remains possible that food will adversely affect reproduction and growth during the population decline at Kluane.

We cannot distinguish between the second and third interpretations above from our experimental results. An experiment designed to separate the effects of density and food on hare demography is necessary to examine the relative effects of these factors. In the only experimental study examining the effects of density on hare demography, Vaughan & Keith (1981) concluded that density *per se* had little effect on hare reproduction, growth or survival. However, their 'low density' treatment was 4·2 hares $\mathrm{ha^{-1}}$, or about 1·5 times the mean autumn density of hares observed at peak numbers on the food grids, and 2·4 times that observed on the controls (density was calculated for our Yukon data by adding a boundary strip of 90 m around the grids to correct for edge effect; see Bondrup-Nielsen 1983; Boutin 1984c). Their 'high density' treatment was 13·2 hares $\mathrm{ha^{-1}}$, or about 4·6 times the mean autumn densities observed on the food grids. A factorial experiment designed to look at the relative effects of food and density-related factors at the lower densities observed at Kluane would better indicate their influence on hare demography. Direct measures of rates of social interaction (e.g. by direct observation), indices of stress (e.g. physiological responses to artificially induced stress), parasite loads and demographic parameters could be made on captive hare populations stocked at different densities and supplied with food at different levels.

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

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