

The interactive effects of food and predators on reproduction and overwinter survival of arctic ground squirrels

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Summary

1. We examined the effects of food and predators on population limitation in the arctic ground squirrel (*Spermophilus parryii plesius* Richardson) in the boreal forest of the south-western Yukon. We focused on ground squirrel reproduction and overwinter survival.

2. Squirrel populations were monitored by live-trapping and radio-telemetry from 1993 to the spring of 1996 on four control and four experimental areas (one predator exclusion treatment, two food addition treatments, and one predator exclusion plus food addition treatment).

3. Predator exclusion increased body condition, percentage lactating, percentage weaning litters, litter size, and doubled population density relative to controls, but had no effect on juvenile growth rate, overwinter survival, or juvenile emergence date.

4. Food addition advanced juvenile emergence date and increased adult body condition, percentage lactating, percentage weaning litters, litter size, population density relative to controls (4–7 fold), but had no effect on juvenile growth rate or overwinter survival.

5. Predator exclusion combined with food addition increased adult body condition, percentage lactating, percentage weaning litters, and population density relative to controls (19-fold).

6. We conclude that arctic ground squirrels in the boreal forest are limited by an interaction between food and predation, acting primarily through changes in reproduction, and that their impact on density was multiplicative.

Key-words: overwinter survival, population limitation, reproduction, *Spermophilus parryii*, sublethal effects of predators.

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Introduction

Both food (Boutin 1990; Sullivan 1990) and predation (Sinclair, Olsen & Redhead 1990; Hanski & Korpimäki 1995; Reid, Krebs & Kenney 1995; Korpimäki & Norrdahl 1998) have been well docu-

mented as independent factors limiting animal populations. Limiting factors are those causing changes in production or loss within a population (Sinclair 1989). Studies examining simultaneous effects of food and predation on populations (Boutin *et al.* 1986) and interactive effects between these factors (McNamara & Houston 1987; Desy, Batzli & Liu 1990; Anholt & Werner 1995; Krebs *et al.* 1995) are rare even though there is consensus on the importance of multifactor limitation (Lack 1954; Sinclair 1989; Mitchell, Arthur & Farrow 1992; Holmes 1995). Single factor approaches to studying population regulation can reveal information about the

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dynamics of a species, but complex interactions with other factors can make the interpretation of single factor effects difficult or, at best, partial. For example, in Boutin's (1990) review of the effects of food supplementation on terrestrial vertebrates, food addition studies generally increased populations two-fold through changes in rates of reproduction, immigration and survival, but patterns of population dynamics were not altered. One explanation was that other factors become limiting after populations double. The effects of predators on vertebrate prey populations are not as consistent as are effects of food addition. Although predators have been shown to limit and sometimes regulate prey populations (Sinclair *et al.* 1990; Pech *et al.* 1992; Korpimäki 1993; Sinclair & Pech 1996), predators sometimes have little effect on prey dynamics (Boonstra 1977; Skogland 1991) or the effect only occurs when prey densities are low and other regulating mechanisms dominate when prey densities are high (Pech *et al.* 1992).

The role of both food and predation in the regulation of terrestrial vertebrates in the boreal forest of the south-west Yukon was the major focus of the Kluane Boreal Forest Ecosystem Project (Krebs *et al.* 1995). This study involved the manipulation of predators and food over a 10-year period from 1987 to 1996. Krebs *et al.* (1995) concluded that food and predation together had more than an additive effect on snowshoe hare populations (*Lepus americanus* Erxleben), suggesting that population cycles of snowshoe hares were caused by a three trophic level interaction. Small mammals [voles (e.g. *Clethrionomys rutilus* Merriam and *Microtus* spp.)], red squirrels (*Tamiasciurus hudsonicus* Erxleben), and arctic ground squirrels (*Spermophilus parryii plesius*) were also subjected to the same manipulations at Kluane. Only arctic ground squirrel populations fluctuated in synchrony with hares and responded to the experimental manipulations (Boutin *et al.* 1995; Hubbs & Boonstra 1997). Hubbs & Boonstra (1997) demonstrated that during the population decline, arctic ground squirrels were food limited, but they concluded that predation interacted with food in limiting populations. However, their evidence of this interaction was weak since only the final year of their 3-year study showed an interactive effect. Byrom (1997) examined changes in rates of survival and population growth and also concluded that an interaction between food and predators occurred during the subsequent increase, as neither food nor predation alone could account for the differences in population densities observed among experimental treatments. In the present paper we examine, separately and combined, the impacts of food and predators on reproductive processes and overwinter survival.

STUDY SPECIES

The arctic ground squirrel has the northern-most distribution of all species of ground squirrel (*Spermophilus* spp.), extending throughout the mainland arctic tundra of Canada, Alaska and eastern Siberia and south into the northern boreal forests (Howell 1938; Banfield 1974; Nadler & Hoffmann 1977). Breeding commences in late April shortly after emergence from an 8–9 month hibernation period (Hock 1960). Young are born in mid to late May and appear above ground close to weaning in mid to late June (Mayer & Roche 1954; Lacey 1991). Dispersal of juvenile males occurs in July (Lacey 1991; Byrom 1997). Hibernation in females begins in late July to late August for adults and juveniles, respectively, followed by males in September (McLean & Towns 1981a). Unlike populations in the boreal forest, those in the arctic or alpine tundra are reported to be stable from one year to the next and appear to be limited by food, burrow availability and spacing behaviour (Carl 1971; Green 1977; Batzli & Sobaski 1980). Carl (1971) regarded the role of predators as only removing the surplus of squirrels that would otherwise be forced to disperse from the best quality habitats.

Study site and methods

STUDY AREA

The study was located along the Alaska Highway within the Shakwak Trench east of Kluane Lake in the south-western Yukon Territory, Canada (61°N, 138°W). There are three major vegetation types in this valley: white spruce forests (*Picea glauca* Blake) cover 50% of the area and have an understorey of willow (*Salix* spp.) and birch (*Betula glandulosa* Raup); shrub meadows of willow and birch cover 33%; and grass meadows cover 7% (Boutin *et al.* 1995); trembling aspen (*Populus tremuloides* Michx.) stands (10%) are sparsely distributed among the three main vegetation types (C.J. Krebs, personal communication).

The Kluane Lake area experiences a mean annual temperature of -3.9 ± 0.2 °C and receives an average 284 ± 10 mm total annual precipitation (data from Burwash Landing Climatological Station 1967–95). The climate is classified as cold continental and snow cover exists from October to early May (Boutin *et al.* 1995).

EXPERIMENTAL DESIGN

In addition to four 8–10 ha control areas that were used to estimate variation in natural populations, we also monitored four experimental areas as follows:

1. *Food addition.* From 1988 to March 1996 *ad libitum* supplemental food (commercial rabbit chow; 16% protein; Shur-Gain, Maple Leaf Foods Inc. Edmonton, Alberta) was added to two 36 ha areas (Food 1 and Food 2). Approximately 300 kg were distributed every 5–6 days throughout the entire year so that food availability would be continuous (Hubbs & Boonstra 1997).

2. *Predator exclosure.* A 1-km² area was enclosed within a 2.2-m high 8600 V electric fence in 1987 to keep out large mammalian predators (lynx [*Lynx canadensis* L.] and coyotes [*Canis latrans* Say]), but it was not a barrier to squirrel movement. One year later, a 9-ha portion of the 36 ha snowshoe hare trapping grid nested within the exclosure was covered with a barrier of nylon monofilament (2 m above ground spaced 20 cm apart) to exclude avian predators. A ground squirrel trapping grid was located under the monofilament. The monofilament was not effective at eliminating avian predation in the monofilament area on snowshoe hares (C.J. Krebs, personal communication) nor on red squirrels (K. Stuart-Smith & S. Boutin, personal communication) but nearly eliminated avian predation on ground squirrels that remained under the monofilament (Byrom 1997). However, within the rest of the exclosure (91 ha), ground squirrels were still subject to avian predation. The fence was effective at keeping out mammalian predators (Krebs *et al.* 1995) and no squirrel was killed within the fence because of mammalian predators (Hubbs & Boonstra 1997; Table 3).

3. *Predator exclosure & food addition.* The above two treatments were combined on a 1-km² area in 1988 using the same protocols described above. A monofilament barrier was not erected and thus this treatment was strictly a mammalian predator exclosure.

PROCEDURES

Live trapping commenced from early April to early May, and ended in late August in all years. Study sites were trapped on average every 2 weeks with more frequent trapping during the emergence of juveniles (young of the year) above ground. Squirrels were captured using Tomahawk live traps (14 × 14 × 40 cm; Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA) baited with peanut butter. Traps were placed only at burrow sites to increase recaptures of individuals. Two or three traps were placed at burrow systems that had ≥ 3 burrow openings. Traps were set at 08.00 h and were checked twice at 1–1.5 h intervals. Each squirrel was removed from the trap into a netted bag and marked in each ear with uniquely numbered metal eartags. At each capture we recorded eartag number, sex, weight, zygomatic arch breadth, and repro-

ductive status. Females were recorded as lactating (nipples large and secreting milk) or not lactating (nipples small or dried).

Population censuses were conducted twice each year: the first, to obtain overwinter survival and spring densities, occurred in a 2–3-week period starting the second week of May, while the second census, to obtain postreproduction and prehibernation densities, occurred from mid-July into the first week of August. Population estimates and standard errors were estimated using a mark–recapture heterogeneity (jackknife) model (Pollock *et al.* 1990) from Program Capture (Otis *et al.* 1978) as recommended by Menkens & Anderson (1988) and Boulanger & Krebs (1994).

We fitted radio-collars (Model PD-2C, Holohil Systems Ltd, Carp, Ontario, Canada) to adult females shortly after spring emergence from hibernation to monitor summer survival (Byrom 1997), locate natal burrows, and monitor fates between field seasons.

Overwinter survival was calculated from trapping records to increase sample sizes and compare our results to the previous results of Hubbs & Boonstra (1997). Owing to male-biased dispersal patterns and small sample sizes for males, we limited our analysis of overwinter survival to adult and juvenile females. Overwinter survival was calculated as the proportion of animals caught during the last week of July (for adult survival), or August (for juvenile survival) that were recaptured in the following year.

To determine weaning success and litter size we needed to locate natal burrows. Burrow sites belonging to radio-collared females were located at night during the first week of June, just prior to the first emergence of juveniles. Within a week of the first sign of juvenile emergence, intensive trapping occurred at these burrows using as many as 10 traps per burrow site in order to capture all of the juveniles born to that female. Juveniles typically remain close to the natal burrow for the first week (Lacey 1991). However, some mothers move their young immediately upon emergence to their adjacent burrow system (McLean 1981b). In high density areas, adult females shared burrow systems and mixing of 2–4 litters in close approximation sometimes occurred before all littermates were captured. When this occurred, all juveniles from the mixed litters were captured. Litter sizes for each treatment were estimated by dividing the total number of juveniles caught at these targeted burrow systems by the total number of breeding females that lived within targeted burrow systems. No measurement of error could be assigned to the estimate because we could not measure each litter separately. The weaning rate of the population was calculated as the percentage of females (lactating and not lactating) that had litters that appeared above ground.

STATISTICAL ANALYSIS

All statistical tests were performed according to procedures in Zar (1984) and Sokal & Rohlf (1995). Binary data (overwinter survival, lactation, and weaning) were analysed by logistic regression using likelihood ratios to test for effects as implemented in JMP (SAS Institute Inc. 1994). Prior to ANOVA and ANCOVA, *F*-tests for equality of variance were performed using StatView (Roth *et al.* 1994). Juvenile growth rates were log transformed, as they did not conform to equality of variance. All other continuous variables satisfied this criterion. ANOVA, post-hoc tests (Tukey–Kramer), ANCOVA, and *t*-tests were performed with SuperANOVA (Gagnon *et al.* 1991). Multiple comparisons after ANCOVA were conducted using *t*-tests on least squares means after adjusting the significance level with a Bonferonni correction. Power analyses were performed using GPower (Buchner, Faul & Erdfelder 1997). All means are expressed as ± 1 SE.

Results

POPULATION CHANGES

Changes in spring breeding population densities of arctic ground squirrels from 1990 to 1996 are shown in Fig. 1. After all control and experimental populations declined from 1991 to 1993, population densities then increased but diverged from one another dramatically, especially those on the Predator Exclusion + Food which attained a density of 30.1 squirrels per ha (Fig. 1). By spring 1996, population densities on the Predator Exclusion, Food 2, Food 1, and Predator Exclusion + Food treatments were 2.0, 3.7, 7.3, and 19.0 times that of our four control sites.

ADULT CONDITION

Body condition for adult female squirrels, as measured by body mass adjusted for skeletal size, was estimated immediately after parturition (mid – late May). Dobson (1992) and Dobson & Michener (1995) demonstrated in Richardson's ground squirrels that this timing provided the best estimate of physiological condition. Body condition of adult males was estimated from the first week of May as this period provided the largest sample size allowing us to compare across treatments. Skeletal size (as measured by zygomatic arch breadth) differed among treatments for both sexes (one-way ANOVA: females: $F_{2,274} = 17.3$, $P = 0.0001$; males: $F_{2,63} = 5.1$, $P < 0.01$) so size was used as a covariate for body mass in an ANCOVA since body mass varies with skeletal size and skeletal size alone is a poor indicator of body condition (Dobson 1992; Dobson & Michener 1995).

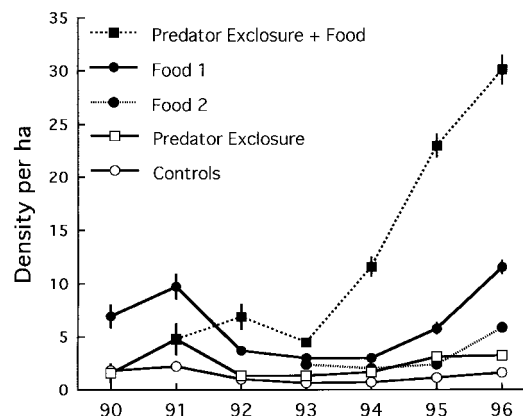


Fig. 1. Spring breeding population densities (\pm SE) of arctic ground squirrels from 1990 to 1996. Points without error bars have very narrow SE values obscured by the point itself. Data from 1990 to 1992 are from Hubbs & Boonstra (1997).

Zygomatic arch breadth was a significant predictor of body mass (Table 1) for both sexes. Body mass for both sexes differed significantly among treatments and years, but there were no significant interaction effects (Table 1). Adult females were significantly heavier in 1994 (529 ± 7 g) than in either 1993 (495 ± 8 g) or 1995 (500 ± 7 g). Adult female mass differed significantly among treatments, except for females on Food and Predator Exclusion treatments, which had similar masses in all years (Table 1). For adult females, body mass is ranked as follows: Predator Exclusion + Food > Food = Predator Exclusion > Controls. Adult males were significantly heavier in 1994 (580 ± 15 g) and in 1995 (599 ± 15 g) than in 1993 (502 ± 18 g). For adult males, food grids generally had significantly larger males while predator exclusion had no effect on male mass (Table 1). Body mass for adult males is ranked as follows: Predator Exclusion + Food = Food > Controls = Predator Exclusion.

REPRODUCTION

Lactation

From 1993 to 1995, at least 77.4% of females on each site gave birth as shown by percentage lactating (Table 2). There was no significant difference in the proportion of females lactating among treatments ($\chi^2 = 3.87$, d.f. = 3, $P = 0.28$) or years ($\chi^2 = 3.60$, d.f. = 2, $P = 0.17$), nor was there an interaction effect ($\chi^2 = 7.93$, d.f. = 6, $P = 0.24$). Since some adult females were used in more than one year, we violated the assumption of independence and hence analysed each year separately. Again, there were no significant differences among treatments in any year (1993, $\chi^2 = 1.79$, d.f. = 3,

Table 1. Spring mass (g) of adult arctic ground squirrels when adjusted for skeletal size differences as measured by zygomatic arch breadth (mm). Females were measured at approximate parturition date while males were measured in the first week of May. Identical superscript indicates differences in mean mass that are not significant. Mean mass for each treatment are calculated from least squares (LS) such that each value given corresponds to the average zygomatic arch breadth for each sex separately (Females = 37.0 ± 0.1 mm; Males = 39.5 ± 0.6 mm)

Year	Controls			Predator Exclusion			Food			Predator Exclusion + Food		
	Mass	Arch	<i>n</i>	Mass	Arch	<i>n</i>	Mass	Arch	<i>n</i>	Mass	Arch	<i>n</i>
Female												
1993 ^a	458 ± 23	35.6 ± 0.8	9	487 ± 24	35.9 ± 0.4	10	506 ± 11	36.9 ± 0.3	24	549 ± 16	37.6 ± 0.3	16
1994 ^b	498 ± 28	35.6 ± 0.3	13	633 ± 67	35.6 ± 0.1	10	527 ± 11	37.5 ± 0.2	28	558 ± 7	37.1 ± 0.3	56
1995 ^a	448 ± 15	36.0 ± 0.3	20	522 ± 29	36.3 ± 0.3	7	523 ± 8	37.6 ± 0.2	55	512 ± 10	37.5 ± 0.3	32
LS Mean	465 ± 9 ^a	35.8 ± 0.2	42	508 ± 11 ^b	35.9 ± 0.2	27	520 ± 6 ^b	37.4 ± 0.1	107	543 ± 6 ^c	37.3 ± 0.2	104
Male												
1993 ^a	422 ± 38	37.4 ± 1.3	3	493 ± 44	40.0 ± 0.6	2	540 ± 28	39.0 ± 0.8	5	614 ± 17	40.0 ± 0.6	14
1994 ^b	608 ± 36	39.4 ± 0.5	3	526 ± 32	37.8 ± 0.3	4	604 ± 23	38.4 ± 1.2	8	638 ± 17	37.8 ± 0.3	14
1995 ^b	584 ± 31	39.6 ± 1.1	4	522 ± 28	39.5 ± 0.5	5	604 ± 26	42.6 ± 0.4	7	625 ± 27	39.5 ± 0.5	6
LS Mean	538 ± 20 ^{a,b}	38.9 ± 0.6	10	514 ± 21 ^b	39.0 ± 0.4	11	583 ± 14 ^{a,c}	40.0 ± 0.7	20	625 ± 12 ^c	39.5 ± 1.2	34

Two-way ANCOVA

	Female			Male		
	<i>F</i>	d.f.	<i>P</i>	<i>F</i>	d.f.	<i>P</i>
Covariate: zygomatic arch	109.0	1	0.0001	15.8	1	0.0002
Treatment	15.0	3	0.0001	8.4	3	0.0001
Year	6.8	2	0.002	7.0	2	0.002
Treatment × Year	1.6	6	0.16	7.8	6	0.11

$P = 0.62$; 1994, $\chi^2 = 4.80$, d.f. = 3, $P = 0.19$; 1995, $\chi^2 = 3.61$, d.f. = 3, $P = 0.31$).

Timing of emergence

Juveniles on controls first emerged on a mean date of 16 June with no more than 7 days difference among years, except in 1992 when inclement spring weather delayed emergence by 18–30 days beyond the mean emergence date (Hubbs & Boonstra 1997). Juveniles on food-supplemented sites emerged 8–10 days earlier than did juveniles on non-fed sites (Table 2). Only in 1992 and 1993 were emergence dates for the food-supplemented sites similar to those on non-fed sites (Fig. 2). There was essentially no difference in emergence dates between the Predator Exclusion and controls and only a slight advancement of emergence date on the Predator Exclusion + Food site in comparison to the food addition sites (Table 2).

Weaning success

We examined the proportion of females that were successful in weaning a litter with a logistic regression model by fitting the presence/absence of litter to two independent variables, year and treatment. Treatments differed significantly from each other ($\chi^2 = 14.7$, d.f. = 3, $P = 0.002$), but years did not

($\chi^2 = 0.2$, d.f. = 2, $P = 0.91$) and neither was there an interaction effect ($\chi^2 = 4.6$, d.f. = 6, $P = 0.58$). The percentage of females weaning a litter (Table 2) when ranked from greatest to least were as follows: Predator Exclusion + Food > Food > Predator Exclusion > Controls.

We used the residuals of body mass at parturition on zygomatic arch to examine the condition of females that would successfully wean litters with those that would not. We limited our analysis to Controls because nearly all females on food-supplemented sites and most on the Predator Exclusion weaned litters. We found that size (zygomatic arch) did not differ between successful and unsuccessful females (two-way ANOVA, $F_{1,38} = 1.28$, $P = 0.27$) or between years (two-way ANOVA, $F_{2,38} = 0.47$, $P = 0.63$). Although the average condition of females varied with year (Table 1), females that weaned young were significantly heavier at parturition (+ 11 ± 13 g) than those who did not wean young (− 23 ± 14 g) (two-way ANOVA, $F_{1,38} = 6.15$, $P < 0.02$) in all years. Thus, females with greater mass have a greater probability of successfully weaning their litter.

Litter size

Mean litter size ranged from 2.8 to 5.0 young per female among our sites. When litter sizes were aver-

Table 2. Reproductive patterns for arctic ground squirrels on all experimental treatments

	Year	Controls	<i>n</i>	Predator Exclosure	<i>n</i>	Food	<i>n</i>	Predator Exclosure + Food	<i>n</i>
Females lactating (%)	1993	77.7	11	90.9	11	86.8	38	89.5	19
	1994	87.5	16	100.0	15	83.0	47	86.9	61
	1995	77.4	31	78.3	23	90.0	70	86.2	109
	Mean	80.9		89.7		86.6		87.5	
Litters weaned (%)	1993	42.9	7	70.0	10	85.7	21	72.7	11
	1994	41.7	12	78.6	14	77.7	18	86.6	15
	1995	52.2	23	69.2	13	67.9	28	90.9	22
	Mean	45.6		72.6		77.1		83.4	
Litter size*	1993	4.2	6	2.8	8	3.9	14	4.5	15
	1994	2.7	9	4.1	8	4.1	21	5.0	25
	1995	3.8	14	4.7	10	4.2	20	3.2	26
	Mean	3.6		3.9		4.1		4.2	
Earliest date of juvenile emergence	1993	14 June		18 June		14 June		7 June	
	1994	13 June		13 June		6 June		6 June	
	1995	20 June		20 June		5 June		6 June	
	Mean	16 June		17 June		8 June		6 June	

aged across years the treatments are ranked as follows: Predator Exclosure + Food > Food > Predator Exclosure > Controls. However the differences between treatments were small (2% to 17%) and the order was not consistent among years (Table 2). We also tested the effects of food addition on litter size by comparing embryo scars from females collected within the food addition treatment but off the census area with road killed squirrels collected from the Alaska Highway. There was no significant difference ($t = 0.14$, d.f. = 12, $P = 0.89$) between embryo counts in food-supplemented squirrels (5.8 ± 0.31 , $N = 6$) and Alaska Highway squirrels (5.8 ± 0.45 , $N = 8$). Thus, litter size *in utero* was not affected by food addition, but litter size at weaning was slightly increased.

JUVENILE GROWTH RATES

We performed a simple linear regression of body mass on time for each juvenile squirrel to calculate growth rate from time of emergence until mid-August. Linear models fit juvenile growth rates for arctic ground squirrels better than exponential models (Hubbs & Boonstra 1997). We included only individuals that were captured and weighed ≥ 3 times with each capture being at least 1 week apart. Our criterion is less stringent than that of Hubbs & Boonstra (1997) who limited their analysis to individuals caught ≥ 5 times. Low population sizes on some sites during our study resulted in an insufficient number of squirrels captured ≥ 5 times. Nevertheless, our estimates of growth rates (Table 3) are similar to those reported by Hubbs & Boonstra (1997).

Since males grew 1.6 g day^{-1} more than females ($7.0 \pm 0.2 \text{ g day}^{-1}$ ($N = 94$) vs. $5.4 \pm 0.1 \text{ g day}^{-1}$

($N = 164$), respectively; one-way ANOVA: $F_{1,256} = 38.06$, $P = 0.0001$], we analysed each sex separately and performed two-way ANOVAs (year \times treatment) on log-transformed growth rates. Females grew significantly more slowly in 1995 ($5.0 \pm 0.2 \text{ g day}^{-1}$) and in 1993 ($5.7 \pm 0.4 \text{ g day}^{-1}$) than in 1994 ($5.9 \pm 0.2 \text{ g day}^{-1}$). Female growth rate differed significantly among treatments (Table 3) with females on the Predator Exclosure treatment growing at a significantly slower rate than those on the Food treatments. Growth rate of juvenile females is ranked by treatment as follows: Food > Controls > Predator Exclosure + Food > Predator Exclosure. Males also grew more slowly in 1995 ($6.0 \pm 0.2 \text{ g day}^{-1}$) than in either 1993 ($7.0 \pm 0.2 \text{ g day}^{-1}$) or 1994 ($8.2 \pm 0.6 \text{ g day}^{-1}$) (Table 3). Male growth rate was not affected by experimental treatment, though the ranking is similar to that for juvenile females: Food > Controls > Predator Exclosure > Predator Exclosure + Food. However, given the increased variation, we had only 5% power to pick up the maximum 15% differences in male growth rates among treatments.

OVERWINTER SURVIVAL

Estimates of overwinter survival using trapping data may be negatively biased if animals disappear before or after hibernation, and not during it. We tested for this by examining fates of squirrels that wore radio-collars overwinter. From 1993 to 1996, only six of 101 radios still transmitting in spring belonged to squirrels that dispersed or died outside of the hibernation period. One adult female moved 60 m outside the trapping area and one yearling male dispersed several kilometers in spring before trapping began. The low frequency of other causes of disap-

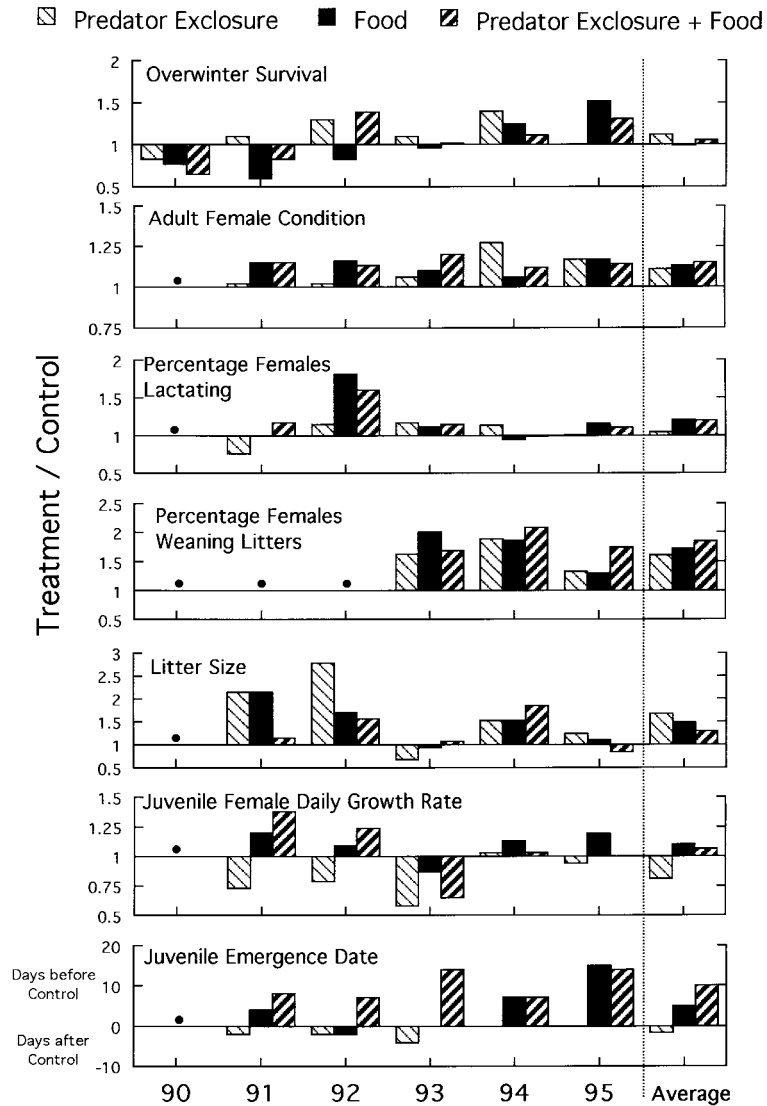


Fig. 2. Ratios of treatment effects to controls. Ratios were calculated by dividing treatment value by control value, except for juvenile emergence date, where the absolute difference (treatment minus control) is presented. Ratios greater than one indicate a positive effect of treatment. Data are shown only for females. Data prior to 1993 are from Hubbs & Boonstra (1997).

pearance indicates that our trapping records should provide a reliable estimate of overwinter survival. Due to male-biased dispersal patterns and small sample sizes for males we limited our analysis of overwinter survival to adult and juvenile females.

Overwinter survival of adult and juvenile females determined from trapping data from four winters (winter 1992/93 to winter of 1995/96) were recorded as binary data (alive = 1, dead = 0) and were used in a logistic regression with the factors age (adult and juvenile), treatment and year as the main effects. Age did not contribute significantly to the two-factor model ($\chi^2 = 0.03$, d.f. = 1, $P = 0.86$). Years differed significantly from one another ($\chi^2 = 10.3$, d.f. = 3, $P = 0.02$) but treatment did not ($\chi^2 = 3.3$, d.f. = 3, $P = 0.35$), and there was no interaction effect ($\chi^2 = 14.4$, d.f. = 9, $P = 0.11$). The differences

in survival among years were primarily due to the winter of 1993/94 when survival on the Food and Predator Exposure + Food treatments experienced a reduction in overwinter survival that contributed to the lowest overall survival during that winter (Table 4). We recalculated overwinter survival from Hubbs & Boonstra (1997) for the years 1990–92 using our procedure to be consistent with our estimates from 1992 to the fall of 1995. When we analysed all years from 1990 to autumn 1995 we found that the main effects, year and treatment, were complicated by a significant interaction ($\chi^2 = 32.6$, d.f. = 15, $P = 0.005$) owing to low survival during the winter of 1991/92 on the food treatment [see Hubbs & Boonstra (1997) for explanation]. Differences among years remained significant ($\chi^2 = 15.5$, d.f. = 5, $P = 0.008$) whereas differences

Table 3. Growth rate (g per day \pm SE) of juvenile arctic ground squirrels from emergence (mid-June to mid-August). Identical superscript indicates means that are not significantly different

Sex	Year	Growth rate (g day ⁻¹) ($X \pm$ SE)							
		Controls	<i>n</i>	Predator Exclosure	<i>n</i>	Food	<i>n</i>	Predator Exclosure + Food	<i>n</i>
Female	1993 ^{a,b}	7.8 \pm 1.3	4	4.5 \pm 0.4	4	6.8 \pm 0.5	4	5.1 \pm 0.4	12
	1994 ^a	5.6 \pm 0.3	5	5.8 \pm 0.3	13	6.3 \pm 0.3	13	5.8 \pm 0.3	29
	1995 ^b	4.8 \pm 0.5	6	4.5 \pm 0.2	20	5.7 \pm 0.3	31	4.8 \pm 0.3	27
	LS Mean	6.0 \pm 0.4 ^{a,b}	15	4.9 \pm 0.3 ^a	37	6.2 \pm 0.3 ^b	48	5.2 \pm 0.2 ^{a,b}	68
Male	1993 ^a	9.2 \pm 0.6	3	6.8 \pm 0.7	3	7.7 \pm 0.7	8	6.7 \pm 0.2	10
	1994 ^a	9.0 \pm 1.5	3	8.6 \pm 0.5	12	9.0 \pm 1.2	12	6.5 \pm 0.8	9
	1995 ^b	4.3 \pm 0.5	3	6.0 \pm 0.3	13	6.1 \pm 0.4	17	6.4 \pm 0.7	7
	LS Mean	7.4 \pm 0.7 ^a	9	7.1 \pm 0.5 ^a	28	7.6 \pm 0.4 ^a	36	6.6 \pm 0.4 ^a	26

Two-way ANCOVA

	Female			Male		
	<i>F</i>	d.f.	<i>P</i>	<i>F</i>	d.f.	<i>P</i>
Treatment	3.7	3	0.01	0.7	3	0.58
Year	6.6	2	0.002	9.8	2	0.0001
Treatment \times Year	1.2	6	0.3	4.6	6	0.15

among treatments did not ($\chi^2 = 0.5$, d.f. = 3, $P = 0.93$). Survival rates for the treatments when averaged across years ranged from 62.6% for the Predator Exclosure treatment to 64.3% for the Predator Exclosure + Food treatment showing little variation (Table 4). Thus, there was no effect of food or predators on overwinter survival; however, overwinter survival can fluctuate up to \sim 30% from year to year.

Discussion

Our experiment resulted in dramatic differences in population densities of arctic ground squirrels among treatments, and one of the principal mechan-

isms driving these differences were changes in reproductive parameters. Following the pronounced decline of populations on all treatments in 1992, which occurred as a result both of high overwinter mortality and of active-season predation in the second summer of the hare decline (Byrom 1997; Hubbs & Boonstra 1997), squirrel populations on all treatments rebounded and by spring 1996, densities on the Predator Exclosure, the Food Addition, and the Predator Exclosure + Food treatments were 2, 5.5, and 19 times, respectively, those on Control sites (Fig. 1). Thus, predators and food together had a multiplicative, not an additive, effect on arctic ground squirrel densities. What demographic processes were responsible for this effect?

Table 4. Overwinter survival (%) of female ground squirrels over six winters. Estimates include adult females (late July to April) and juvenile females (mid-August to April) combined because overwinter survival is independent of age

Winter	Controls		Predator Exclosure		Food		Predator Exclosure + Food		Weighted mean	
	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>
1990/91*	81.0	21	66.7	33	63.0	27	53.8	39	64.2	120
1991/92*	61.3	31	66.7	18	37.0	54	52.2	46	50.3	149
1992/93	62.5	8	63.6	11	63.6	11	86.7	15	71.1	45
1993/94	58.1	31	61.1	18	54.0	50	56.9	58	56.7	157
1994/95	63.3	30	85.7	21	79.2	48	69.6	69	73.2	168
1995/96	51.6	31	51.5	33	78.5	107	66.7	138	67.6	309
Unweighted mean	63.0		65.9		62.6		64.3		63.8	948

*Recalculated from Hubbs & Boonstra (1997).

All treatments either directly or indirectly improved various aspects associated with reproduction. All treatments improved maternal condition, with females on the Predator Exclusion, Food Addition, and Predator Exclusion + Food averaging 9%, 12%, and 17%, respectively, heavier in spring than females on the Control grids (Table 1). All treatments had 7–11% more females lactating than on Control sites (Table 2), but there were no consistent differences among the treatments. All treatments improved the percentage of females weaning litters, with females on the Predator Exclusion, Food Addition, and Predator Exclusion + Food weaning on average 59%, 65%, and 83%, respectively, more of their litters than females on the Control grids (Table 1, Fig. 2). Of those females that actually weaned litters, the treatments improved litter size at weaning only modestly (by 0.3–0.6 more young weaned per litter). Finally, juveniles on the food-addition treatments emerged about 8–11 days earlier than did those on the non-food treatments (Table 2) and thus, they had a longer active season in which to grow prior to hibernation. However, there were no consistent differences in growth rates among treatments (Table 3). Thus, many aspects associated with reproduction improved as a result of the treatments, but only two (female condition and percentage of females weaning young) showed consistent differences amongst the treatments.

The other key demographic parameter which could have been affected, survival, was not consistently improved as a function of our treatments: neither overwinter survival (Table 4) in all females pooled nor active-season survival of juveniles (Byrom 1997) were improved. However, active-season survival of adults from 1993 to 1995 (Byrom 1997) was higher on the experimental treatments. However, the treatments did not differ markedly from each other and thus this parameter could not explain the multiplicative effect on densities that we observed. This result also implies that raptors, which were the only predators able to hunt squirrels on the predator exclusions, were not able to completely compensate for the absence of mammalian predators. Thus, food and predation interacted primarily through changes in reproduction and in active-season survival of adults, but it was only the former processes which caused the multiplicative density effects. Within a year, the differences among treatments was sometimes small (e.g. percentage litters weaned in 1994), but over time there was a cumulative effect causing the populations to diverge.

One caveat should be addressed. Our experimental manipulations were temporally pseudoreplicated. Replication was exchanged for long-term and large-scale manipulations, hence years were not independent and only the food-addition treatments were replicated ($N = 2$). There are three arguments against

the possibility that effects were a result of location-dependent siting of the various treatments. First, we did replicate the control grids ($N = 4$) to assess natural variation, and it is clear from the very small standard errors (Fig. 1) that the densities on unmanipulated sites were similar and vary little over time. Secondly, all our grids were located on areas of similar habitat (predominantly open spruce and shrub-meadow; Hubbs & Boonstra 1997). Thirdly, marked responses to food addition have been observed in other species of small mammals (Boutin 1990), including ground-dwelling sciurids (Dobson & Kjelgaard 1985a,b; Dobson 1995) and to food addition plus predator exclusion in snowshoe hares (Krebs *et al.* 1995), and thus our findings are not anomalous outliers.

The trade-offs of lack of replication or pseudoreplication are a common problem with long-term whole ecosystem experiments burdened with limited funding (Carpenter *et al.* 1995). In order to detect differences between unreplicated treatments, effects need to be very large in order to overcome natural variation (Carpenter 1990). Our study demonstrated dramatic treatment effects on population densities (Fig. 1). Densities on the Food 1 and Predator Exclusion + Food treatments (11.6 and 30.1 squirrels per ha, respectively) exceeded known maximum densities for unmanipulated arctic ground squirrel populations by up to 14 times [6.6 squirrels per ha, Green (1977); 5.5 per ha Carl (1971); and 2.2 per ha, Hubbs & Boonstra (1997)]. However, two of the factors associated with reproduction (lactation and litter size) showed only small differences within years and were confounded by variability among years (Fig. 2). Only weaning rate showed large differences, at least between treatments and controls (Fig. 2), but this parameter was measured only from 1993 to 1995. Nevertheless, over time, the cumulative effect of these reproductive parameters produced the increased divergence in population densities that we observed among the treatments.

The decline in arctic ground squirrels populations (1991–93) took place when predator densities were high and the subsequent increase in squirrel populations (1993–96) (Fig. 1) took place when predator densities had declined to very low levels. The numbers of the main predators of hares per 100 km² in our study area were as follows: from 1990 to 1992 there were between 48 and 56 great horned owls (*Buteo jamaicensis* Gmelin) and goshawks (*Accipiter gentilis* L.) in the valley, 30 in 1993, 24 in 1994, and 26 in 1995 (F. Doyle, C. Bohner & J. N. M. Smith, personal communication); respective values for lynx and coyotes were 20.0 in 1990, 26.3 in 1991, 12.8 in 1992, 6.8 in 1993, 3.4 in 1994, and 4.0 in 1995 (Boutin *et al.* 1995; M. O'Donoghue *et al.*, personal communication).

Predators may act in a more subtle manner than directly killing their prey. Predators may have sub-

lethal effects, but it has proven challenging for empirical studies to demonstrate these and their role on prey dynamics (Wooster & Sih 1995; Cartar & Smallwood 1996). On Controls, we found that females in better condition (weight in spring at parturition) were more likely to wean their litters. On the Predator Enclosure, we found that female condition averaged 9% higher than on the Controls (Table 1), and thus females on the Predator Enclosure were heavier in each of 6 years of the research (range: 6–27%; Hubbs & Boonstra 1997: Table 8; this study: Table 1). We also found that ground squirrel reproduction increased when large mammalian predators were excluded from an area. Litter sizes were greater on the Predator Enclosure than on the Controls in 4 of the 5 years of the research (Hubbs & Boonstra 1997: Table 5 [1991 and 1992]; this study: Table 2 [1993,95]) (overall mean \pm SE on the Predator Enclosure 3.4 ± 0.4 young per litter vs. Controls: 2.6 ± 0.6) and more females weaned young within the Predator Enclosure (mean = 72%) than on the Controls (45%) (Table 2) (not measured by Hubbs & Boonstra 1997). The same trend in improved weaning rate as a function of the predator fence between the Predator Enclosure and the Controls was observed between the Predator Enclosure + Food and the Food addition site but to a lesser degree (83% vs. 77%, respectively, Table 2). We have no evidence to indicate that this was the result of differences in the quantity or quality of food among these areas nor of differences in direct mammalian predation on the babies in the burrow or immediately on emergence. The only predator that could have potentially entered burrows to kill squirrel babies was the short-tailed weasel (*Mustela erminea* L.), but it was extremely rare; only nine were caught in 10 years (1987–96) on trapping 15 different small mammal grids (R. Boonstra & C. J. Krebs, personal communication). Also, there should have been no differential between fenced and unfenced treatments as the fence did not prevent the weasels from entering the enclosures. Another possibility is that lynx and coyotes killed the babies on the unfenced grids shortly after they emerged from their natal burrows and before we captured them. We do not think this is a significant factor for two reasons. First, we trapped these burrow sites as soon as the young were observed above ground and at least within a week of emergence. Secondly, mammalian predation on juveniles appears more rare than avian predation: of the 60 juveniles radio-collared and killed between 1992 and 95, 79% were killed by avian predators (Byrom 1997). Thus, we think that the causes of the difference in reproduction between unfenced and fenced areas was as a result of the sublethal effects of higher predation risk by mammalian predators on the unfenced treatments.

Anti-predatory behaviours (Holmes 1984; Carey & Moore 1986; Lima 1987) can result in less time spent foraging (Holmes 1991; Kieffer 1991) potentially causing body condition to decline and fecundity to decrease (Hik 1995). For an animal to maximize fitness in the face of high predation risk, it may trade off reproduction for survival (Oksanen & Lundberg 1995), especially for species in which breeding requires more energy than survival and future reproduction is not compromised by making this trade off (Bednekoff 1996). However, convincing evidence of prey making reproductive decisions on the basis of predation risk are rare (Lima & Dill 1990). An alternative hypothesis for the sublethal effects on prey by their predators was put forth by Boonstra *et al.* (1998), and involves the effects of chronic stress. They found that snowshoe hares were chronically stressed during the cyclic decline phase, but not during the following increase phase, and concluded that the most plausible explanation was the high predation risk during the decline. Hares experienced severe effects during the cyclic decline in all physiological measures associated with the stress response (hypothalamic-pituitary-adrenal response, energy mobilization, immune response, mass loss, and reproductive hormone response) and these were associated with the extremely poor reproduction during the decline. Indirect effects of predation risk can effectively scar individuals and influence population dynamics even after predators are gone (Boonstra & Singleton 1993; Hik 1995; Boonstra *et al.* 1998). For arctic ground squirrels it is not clear whether behavioural changes in foraging patterns, physiological stress responses, or both were responsible for the changes in condition and reproduction that we observed when predators were absent from our enclosures. The most likely scenario is that both responses occur simultaneously, but we do not know in what proportion and what the long-term consequences are. Predators may impose long-term sublethal effects on arctic ground squirrels, which may be the reason why predator exclusion effects became more evident during the latter part of the study when differences in population densities between the Predator Enclosure + Food and Food-addition treatments (1996 = 3.4-fold) and between the Predator Enclosure treatment and Controls (1995 = 2.6-fold) became more apparent.

Exclusion of predators improved female condition and reproduction but did not effect overwinter survival (Fig. 2). If reproduction was limited due to reduced foraging rates in the presence of predators then overwinter survival should also be limited by reduced foraging rates. In the face of high predation risk, females can trade off reproduction for survival and another reproductive opportunity (Oksanen & Lundberg 1995; Bednekoff 1996). However, ground squirrels must accumulate sufficient fat reserves or

else perish overwinter. They cannot trade off fat reserves. They may need to accept a higher predation risk to minimize overwinter mortality, a situation analogous to the predation–starvation trade-offs (McNamara & Houston 1987; McNamara & Houston 1990; Sweitzer 1996). Physiological trade-offs also exist where fat accumulation prior to hibernation is important to Belding's ground squirrels (*S. beldingi* Merriam). When these squirrels' foraging times are restricted they lose fat-free mass rather than fat reserves (Bachman 1994). Overwinter survival at all costs may be an important life-history strategy for ground-dwelling squirrels, and may explain why we did not detect any differences in overwinter survival for squirrels whether or not predators were present the previous summer.

Positive effects of food abundance or availability on reproduction have been demonstrated for many species (Arcese & Smith 1988; Doonan & Slade 1995; Duquette & Millar 1995; Rohner & Smith 1996). However, in hibernators, food abundance during the few weeks remaining after reproduction and before winter play a critical role in their ability to survive to the next breeding season. Prior to winter hibernation, ground-dwelling sciurids increase foraging (Armitage, Downhower & Svendsen 1976; Kenagy 1987) resulting in increased fat reserves (Morton 1975; Davis 1976). Successful hibernation is dependent on the quantity of the accumulated fat reserves (Murie & Boag 1984), and thus food can potentially limit populations through overwinter mortality. Although overwinter survival in our study fluctuated from year to year, the effects of the treatments were not consistent (Fig. 2). Our treatments may have been inadequate for accurately testing the role of food on overwinter survival or on the role of overwinter survival on population regulation. Our food addition was sufficient in protein (16%) but may have been lacking in essential nutrients for herbivorous hibernators, which rely on critical fatty acids, so we may have given sufficient food quantity but inadequate food quality. Investigations on yellow-bellied marmots (*Marmota flaviventris* Audubon and Bachman) showed that the composition of fatty acids in the food determines fatty acid composition in white adipose tissue (Geiser 1990) and these are very important in regulating metabolic and thermoregulatory processes during hibernation (Florant *et al.* 1990; Thorp, Ram & Florant 1994). Sciurid hibernators fed diets rich in polyunsaturated fatty acids (i.e. linoleic acid) had lower minimum body temperatures, lower metabolic rates and longer bouts of torpor (Geiser & Kenagy 1987; Frank 1992; Geiser & Kenagy 1993) each of which enhances the probability of overwinter survival.

Polyunsaturated fatty acid content of plants varies greatly with species, season, and among different parts of the plant (Harwood & Geyer 1964; Florant

et al. 1990) and may prove to be a limiting resource for competing herbivore hibernators. Florant *et al.* (1990) suggested that yellow-bellied marmots that have been observed to extend their home range into areas with abundant cow parsnip (*Heracleum lanatum* Michx) (Armitage 1979), may be seeking the high concentrations of linoleic acid contained within that species (Florant *et al.* 1990). If arctic ground squirrel populations are limited by availability of polyunsaturates we would expect reduced overwinter survival in our high-density populations since polyunsaturates were not supplied with the rabbit chow. Competition among squirrels for critical plant resources during the reproductive phase of the active season, may limit the availability of those plants later in the season when squirrels are in the process of accumulating fat reserves. By supplementing food, we may have reduced foraging pressure on natural vegetation early in the season, thus increasing its availability later on when it is needed prior to hibernation. This could indirectly secure supplies of polyunsaturates, thus ensuring overwinter survival despite the relatively low vegetation available per squirrel. Interacting demands for different plant nutrients for reproduction and overwinter survival may play a significant role in population dynamics of herbivorous hibernators.

We have shown that arctic ground squirrel populations in the boreal forest are limited by an interaction between food and predators, acting primarily through changes in reproduction. The cumulative effect over 9 years produced the large differences in population densities within our treatments. However, limiting processes are not necessarily regulating (Sinclair & Pech 1996). By definition, regulation occurs when per capita rates of production or mortality are density-dependent (Sinclair 1989). Our experimental design does not directly test for density dependence or its mechanisms but it does set the stage for an ideal opportunity to do so. The treatments ceased in 1996, thus regulating processes should become evident as arctic ground squirrel populations return to control levels.

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