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The Role of Red Squirrels and Arctic Ground Squirrels

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A consistent feature throughout the boreal forest of North America is the rattle call of the red squirrel, *Tamiasciurus hudsonicus,* as it advertises its whereabouts to conspecifics. Like the snowshoe hare, the red squirrel's distribution encompasses the entire boreal forest (see figure 2.7). The "keek keek" call of a second squirrel species, the arctic ground squirrel (*Spermophilus parryii,* the *siksik* of the Inuit), is also heard in the boreal forests of northwestern North America (Banfield 1974). In terms of biomass of herbivores in these forests, these two squirrels are the second and third most important, respectively, after snowshoe hares (see figure 1.2). Both squirrel species could serve as alternate food sources for the many predators who eat primarily snowshoe hares. However, before our study, no one had investigated experimentally the possible linkages between populations of these squirrels and the snowshoe hare population cycle. The conventional wisdom is that any link would be a secondary one, as predators switch from hares to squirrels during the hare decline. Though both squirrels are active during the summer and thus potentially available to predators, only red squirrels remain active during the long boreal winter and are one of the few alternate prey available to hare predators.

9.1 Natural History

9.1.1 Red Squirrels

Red Squirrels are medium-sized (ca. 250 g) granivores. They defend individual, nonoverlapping territories year-round (C. C. Smith 1968, Price et al. 1986, 1990), which are maintained by means of specialized calls, scent marking, and aggressive expulsion of intruders. Possession of a territory (0.2–0.5 ha) is essential for overwinter survival (Larsen and Boutin 1994). Territory owners rarely lose their territory to another squirrel, but breeding females sometimes bequeath part or all of their territory to one or more of their offspring. If this happens, females seldom move more than one or two territories away. The beauty of this social system for the researcher is that when a squirrel disappears from a territory, one can be almost certain that the squirrel has died. This territoriality, coupled with the fact that squirrels are easily trapped and highly visible, makes for accurate measures of density and survival.

Females can breed when 2 years old and the norm is to give birth to a single litter of 1–6 offspring (mean 2.6 young/female), usually during April and May (Boutin and Larsen 1993). Births are not synchronous, with the first and last litters in a year being separated by 55–82 days (O'Donoghue and Boutin 1995). Young begin to spend time out of the nest at about 42 days and are weaned at about 70 days. Dispersal occurs shortly after weaning, but it is usually to a site within one to two territories of where they were born (Larsen and Boutin 1994). Each territory has a central food cache or midden where 12,000–16,000 unopened conifer cones (white spruce in Kluane) are stored for winter consumption (M. C. Smith 1968, Gurnell 1984, Obbard 1987). Squirrels feed on a wide variety of foods, such as conifer buds and flowers, lichens, berries, mushrooms, insects, bird eggs, young birds, and hare leverets, but their staple food is conifer seed obtained by husking cones. Squirrels begin to consume the seed in July or August when cones are still green. Before this they rely on cones stored from previous years. Cones are not clipped until late August or early September, and harvesting is complete by late September. Cones are stored in a series of shallow underground tunnels, primarily in middens. Once underground, the cones remain closed and can last several years. The cones are also protected from pilfering by mice and voles because these species cannot extract the seed efficiently. The only potential thieves are other conspecifics, and this leads to a strict territorial social system.

9.1.2 Arctic Ground Squirrels

Arctic ground squirrels are medium-sized (ca. 500 g), diurnal, burrowing herbivores adapted for life close to the ground: they are short, stocky, and cylindrical, with strong, powerful claws for digging through soil. The burrow is critical to survival, and possession of a burrow gives ground squirrels protection from both predators and the elements and a place in which to hibernate through the long northern winter. Most of the range of the arctic ground squirrel is in arctic and alpine tundra regions of Canada, Alaska, and Siberia (Nadler et al. 1974, Nadler and Hoffmann 1977). Consequently, most of the research on ground squirrels has been done either there (Carl 1971, Green 1977, Batzli and Sobaski 1980) or in open meadows in the boreal forest (McLean 1981, Lacey 1991). These researchers have concluded that the Arctic ground squirrel populations remain relatively stable over time in these open habitats and that food, spacing behavior, and burrow availability, but not predation, limit their numbers.

Arctic ground squirrels live in small groups of related females (female home ranges of 2.5 ha, densities of 1–3/ha, Hubbs and Boonstra 1997), with no more than one territorial male per group. They are obligate hibernators, emerging above ground from a 7- to 8-month hibernation in early to mid-April, with males appearing about 1–2 weeks before females (Carl 1971, Lacey 1991). Mating occurs within several days of female emergence and is generally highly synchronous. Yearlings are reproductively mature, and thus the entire population breeds each year. Litters of 4–7 (mean 4.9; Hubbs and Boonstra 1997) are born 25 days later and appear above ground in late June. Weaning takes place about 1 week later, and juveniles (primarily males) disperse in July. Adult females usually enter hibernation in late July to mid-August, adult males shortly thereafter, and juveniles as late as September or early October. Arctic ground squirrels eat a large variety of foods, ranging from seeds (*Arctostaphylos* spp.), leaves, and flowers (e.g., *Anemone* spp.) of forbs (especially legume species), mushrooms, and, to a lesser extent, willows leaves and catkins, grasses, and sage (*Artemisia* spp.) (McLean 1985). Like red squirrels, they readily eat animal matter and may kill to get it (e.g., microtines: Boonstra et al. 1990; hare leverets: O'Donoghue 1994). They also readily ate the rabbit chow we distributed on the food supplementation treatments.

9.2 Community Interactions and Factors Affecting Population Dynamics

The populations of these two squirrel species could be responding in one of two ways to the hare cycle. First, they could be driven by forces unrelated to the hare cycle (e.g., stochastic factors such as weather which affect the squirrel populations either directly or indirectly through their effects on food supply) and thus could be operating largely independently of the hare cycle. Indeed, for red squirrels, the general conclusion has been that the strict territoriality in prime habitat maintains population stability, while regional populations fluctuate markedly as a direct consequence of fluctuations in the critical food supply, the conifer cone crop (Kemp and Keith 1970, Rusch and Reeder 1978, Sullivan 1990, Klenner and Krebs 1991). Alternatively, squirrels could be tightly linked to the hare cycle through two major ecological processes, competition and predation. Competition is unlikely to play a significant role, as the niches of squirrels and hares are so different and overlap little. Predation, on the other hand, is more probable, possibly occurring directly as both squirrel species kill and eat hare leverets, particularly at certain times of the cycle (O'Donoghue 1994), and indirectly as predators switch from hares to squirrels during the hare decline. The current evidence is unclear. Both squirrel species are readily preyed upon by all of the predators that eat hares (see chapters 13–16). Anecdotal evidence from the aspen–coniferous forests of Alberta suggests that red squirrels decline after a hare decline (Keith and Cary 1991) and that this is possibly caused by predator switching. The evidence that declines in hares are echoed by declines in ground squirrels is slightly better in those species living along the southern border of the boreal forest (Adamcik et al. 1979, Erlien and Tester 1984, Keith and Cary 1991). Our objectives were to determine (1) whether food, predators, or an interaction between food and predators limited populations of these two squirrel species and (2) whether squirrel survival and density were affected by the snowshoe hare cycle. We deal with each species separately in the Methods and Results and then have a combined Discussion section.

9.3 Methods

9.3.1 Red Squirrels

Population and Survival Estimation Population changes from 1987 to 1996 were determined by a 3- to 5-day trapping session in late May–early June (spring) and another session in late July–early August (summer) on 10 × 10 grids with stations 30 m apart (7.3 ha) on all experimental treatments. We prebaited 50 traps with peanut butter 3–5 days before trapping, placed traps at every other trapping station, and set them at 0700 h. Traps were checked twice and locked open by 1230 h. All new squirrels were tagged in both ears, and on each capture we recorded tag number, location, mass, sex, and breeding condition (males, scrotal or abdominal testes; females, lactating or not). Newly captured squirrels were classified as adult if they weighed more than 200 g. In addition to this trapping, we periodically trapped at middens in autumn (September–October) to obtain a cohort of 20–30 adult squirrels to monitor survival rates over the winter. In some cases these individuals were also radio collared. Middens were retrapped in March and May to determine which squirrels had survived. We calculated survival as the proportion of squirrels still alive at the end of a season.

Intensive Studies on Control and Experimental Sites As part of a long-term study of the behavioral ecology of red squirrels, we monitored squirrels intensively on four grids. This work began in 1987 on control 1, fertilizer 1, and a new grid, control E (figure 9.1). Control 4 was added in 1988. We also followed the predator exclosure grid intensively from summer 1991 through summer 1993 (Stuart-Smith and Boutin 1995). The objective was to enumerate all squirrels with individually numbered tags and color marks, determine the middens owned by each, and follow the reproductive condition of females. All females were monitored closely by trapping and observation during the breeding season (April–August). We located and entered nests to enumerate the young (CD-ROM frame 28). A cohort of squirrels was often radio collared in late August or early September, and their fates were monitored weekly throughout the winter. Details of methods can be found in Boutin and Larsen (1993). Our efforts were largely successful, and we were able to obtain the birth date, midden ownership, and date of disappearance of most squirrels from the grid.

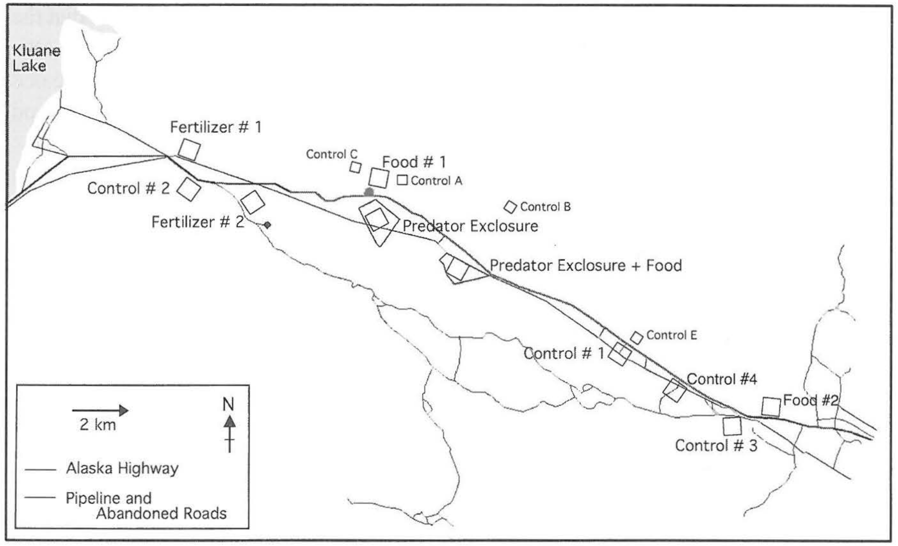

Figure 9.1 Spatial arrangement of treatments and controls at Kluane. Red squirrels were monitored on all experimental treatments and on three controls (1,4, and E). Ground squirrels were monitored on all experimental treatments and on four controls (A–D). Controls C and D were monitored from 1993 onward. Control D is located within Control 3.

The size of the area on which we were able to follow squirrels intensively varied somewhat from year to year. To be consistent, we determined midden ownership changes on a 270 m × 270 m (7.3 ha) grid, which was similar in size and location to the area trapped for population estimation. However, from 1989 onward, we monitored an area at least as large as the entire hare grid (35 ha). We included individuals caught on this area in assessments of adult survival, juvenile production, and juvenile survival.

Our intensive research allowed us to determine the reliability of information obtained from the trapping sessions. We estimated population size using the program CAPTURE (Otis et al. 1978). Confidence limits on the capture estimates were narrow (often 0), and estimates were always within four individuals of the total number of different animals caught each session. In all cases we report the total number. We also estimated population size by recording the number of squirrels that owned middens within the trapping grid. Midden owners and the number caught were highly correlated ($r^2 = .53$; $y = 8.11 +$

0.98x). Estimates of actual density as determined by midden ownership indicated that the 7.3-ha trapping grid effectively trapped an area closer to 10 ha. Thus, we report all estimates of population density as number per 10 ha. The extensive research also revealed that squirrels that disappeared from their middens could be considered dead (Larsen and Boutin 1994).

Finally, the extensive trapping was largely ineffective as a means of enumerating or indexing juvenile production and early survival. Juvenile squirrels are difficult to catch for the first time, so it takes a considerable amount of exposure to traps. Also, the date of emergence of juveniles can vary by as much as 6 weeks from year to year. For example, in 1994, many young were old enough to be trapped in the May session, whereas in most years they are not present until late July, and in some cases (e.g., 1990) many have not emerged until mid August. Our work schedule at Kluane did not allow us to vary the timing of trapping, so relatively few juveniles were captured in the late summer session. As a consequence, we only report measures of juvenile production from the intensively studied grids.

9.3.2 Arctic Ground Squirrels

Population and Survival Estimation Ground squirrels were monitored intensively for 7 consecutive years (1990–1996) on 10 × 10 grids with stations 30 m apart (see Hubbs and Boonstra 1997 for details). Because the experimental treatments effectively ceased for arctic ground squirrels in late winter 1995–1996, the presentation of the results of the treatment effects concentrates on the period when the treatments were in place (1990–1995). Over this period, we captured 8758 ground squirrels on all control grids and experimental grids combined. Though minimal trapping occurred from 1987 to 1989, the intensity was not sufficient to assess population parameters, and thus we ignore these years. All treatment and control populations were censused twice per year using Tomahawk live traps, and additional trapping occurred throughout the active season on all grids except on the fertilizer treatments. From 1990 to 1992, two control grids (A and B) were trapped, and from 1993 to 1996, two additional control grids (C and D) were added (figure 9.1). On the experimental treatments, the trapping grids were nested within the snowshoe hare trapping grids. We tagged all new squirrels in both ears and on each capture recorded tag number, location, mass, sex, and breeding condition (males, scrotal or abdominal testes; females, lactating or not). All populations were censused once in spring (May 1–15) to assess spring densities and overwinter survival and once in summer (July 14–31) to assess densities before hibernation but after reproduction and juvenile dispersal. To assess reproductive parameters, an additional intensive trapping targeting juveniles occurred at natal burrows in June just after juvenile emergence.

Two main trapping methods were used:

1. Burrow trapping. From 1990 to 1992, adult squirrels were trapped at their burrows. One trap was placed at each burrow entrance, and two to three traps were placed at large, perennial burrow systems with multiple entrances. Traps were baited with peanut butter, set at 0800 h, checked twice per morning at 2-h intervals, and closed at 1200 h (Hubbs and Boonstra 1997). We trapped squirrels for 2 consecutive days (to give a total of four trapping sessions) and estimated population densities with the program CAPTURE (Otis et al. 1978).

2. Stake trapping. From 1993 to 1996 we trapped squirrels at alternate grid stakes both to maximize our efficiency as density increased on some treatments and to simultaneously assess red squirrel numbers. Traps were set at 0700 h, checked three times at 1.5-h intervals, and closed by 1230 h. Captures from the three daily checks were pooled to give an overall daily capture rate. This procedure was repeated for at least 3 consecutive days until the population estimate had an associated standard error of $\leq$10%. We calculated estimates using the mark–recapture heterogeneity (jack knife) model (Pollock et al. 1990) of CAPTURE (Otis et al. 1978), as recommended by Menkens and Anderson (1988) and Boulanger and Krebs (1994). We are confident that this trapping method produced robust demographic information for two reasons: first, trappability of arctic ground squirrels is high (77% for adults and 88% for juveniles; Hubbs and Boonstra 1997); and second, there was no bias in estimates as the density increased (i.e., the relationship between the estimate and the numbers actually caught was linear over a range of 3–356 squirrels ($r^2 = .995$, $n = 76$, $p < .001$). We tested whether the change from burrow trapping to stake trapping affected estimates by carrying out both techniques sequentially (separated by 3 days) in 1993 on the predator exclosure. There was no difference between methods (burrow trapping: 12 ± 0 [95% CL] vs. stake trapping: 13 ± 0). Finally, on treatments with very high densities (food and predator exclosure + food), traps became saturated when only stakes were trapped and thus trapping occurred at both stakes and burrows to reduce trap competition.

To obtain estimates of survival and home range size, we radio collared squirrels. During the active season, adults were radio collared with 5-g radio collars (PD-2C transmitters, Holohill Systems Limited, Carp, Ontario) and juveniles with 6-g expandable collar radios (SS-2 transmitters with Hg-675 batteries; Biotrack, Dorset, England). Survival of adults (from emergence in April to immergence in August or September) was obtained on a sample of squirrels on each of the treatments (n = 13–30/year/treatment from 1992 to 1995; n = 13–25/year on all four of the control grids combined from 1993 to 1995). Survival of juveniles was obtained on a sample of squirrels from each of the treatments from June to August 1993–1995 (n = 195; Byrom 1997). Adults were located twice per week, and juvenile squirrels were located every 2 days with a hand-held antenna. We estimated survival of adults and juveniles using formulas in Pollock et al. (1989). All survival estimates were compared using a log-rank test (Pollock et al. 1989). For all radio-collared squirrels killed by predators, we identified the predator based on characteristics at the kill site, such as feathers, pellets, whitewash, plucking, or scats.

We calculated overwinter survival of adults and juveniles using radio-collared squirrels from 1993 to 1996 fitted with the same radio transmitter type as used on adults during the summer. Radios with fresh batteries were placed on adults in late July and on juveniles after mid-August. The location of each squirrel was determined by telemetry during mid-February when the squirrels were still in hibernation. From early April, each squirrel was relocated and its fate determined by cross-referencing spring positions to winter hibernacula. If the radio signal remained in fixed location until June and the squirrel was never captured again, the squirrel was recorded not to have survived the winter. Because this method was not used before 1993, we calculated overwinter survival of adult and juvenile females using trapping data to include previous years. Squirrels that were absent in the spring after being recorded during autumn trapping were considered not to have survived the winter.

Reproduction We trapped juveniles as soon as they emerged in June on all experimental treatments and controls; thus we do not know the number born, only the number recruiting to the traps on emergence. Juveniles typically remain close to the natal burrow for the first week (Lacey 1991). However, some mothers move their young immediately upon emergence (McLean 1981) to their adjacent resident burrow system, which may be shared with two to four females in high-density populations. Natal burrows of adult females were identified from a combination of live trapping, visual observations, and radio telemetry. A wire mesh, multiple-capture trap designed specifically to capture juveniles (Waterman 1986) was placed at each natal burrow and adjacent resident burrow, along with two to six Tomahawk traps. On control grids and on the predator exclosure grid, most juveniles at a particular burrow system could be assigned to an individual female. However, an accurate measure of litter size for an individual female was not possible for most females from food-supplemented treatments owing to the high degree of mixed litters because of high density. When this occurred, we estimated litter size by dividing the total number of juveniles caught at these targeted burrow systems by the total number of breeding females that lived within that burrow system.

9.4 Results

9.4.1 Red Squirrels

Population Demography on Control Sites Spring populations of red squirrels from 1987 to 1996 were not correlated with snowshoe hare populations ($r = .14$, $p = .69$, $n = 10$), remaining relatively constant at between 1.5 and 2.8 squirrels/ha (figure 9.2). Population estimates based on midden ownership on the intensively studied control areas indicated that between-site variation was as great as between-year variation (figure 9.3). Densities varied roughly twofold between control 4 (mean = 1.72/ha) and control 1 (mean = 2.74/ha; figure 9.3). These between-site differences were partly a consequence of the amount of usable habitat on each site (50% spruce cover on control 4 as compared to 90% on other controls). All grids showed a slight decline to relatively low values in 1991–1993. This was followed by increases to maximum levels in 1994. Control E showed the largest change, where numbers doubled between 1991 and 1994. All grids showed a brief decline overwinter in 1994–1995. To summarize, red squirrel densities at Kluane were best characterized by their remarkable constancy over the course of the hare cycle.

Like population density, adult survival (per 6 months) showed little variation. It was consistently near 80% in both summer and winter during the study (figure 9.4). The most notable exception was during the summer of 1992, when almost half of the adults disappeared. Survival also dipped to just under 70% over summer 1995. Juvenile survival was more variable, and we examined it by looking first at overall changes from birth to the next spring and then by separating survival into two periods: from birth to emergence from the nest and from emergence to the next spring. Juveniles had an average survival rate from birth to the next spring of 23%, with 1989, 1992, and 1994 being years of particularly poor survival (<15%), and 1991 and 1993 being years of particularly good survival (38–43%; figure 9.5a). Nestling survival was consistently near 70% except in 1992 and 1995, when it dropped below 40% (figure 9.5b). Postemergence survival was extremely low in 1994 (5%), relatively low in 1989 and 1990 (<28%), and high in 1991, 1993, and 1995 (>55%; figure 9.5c).

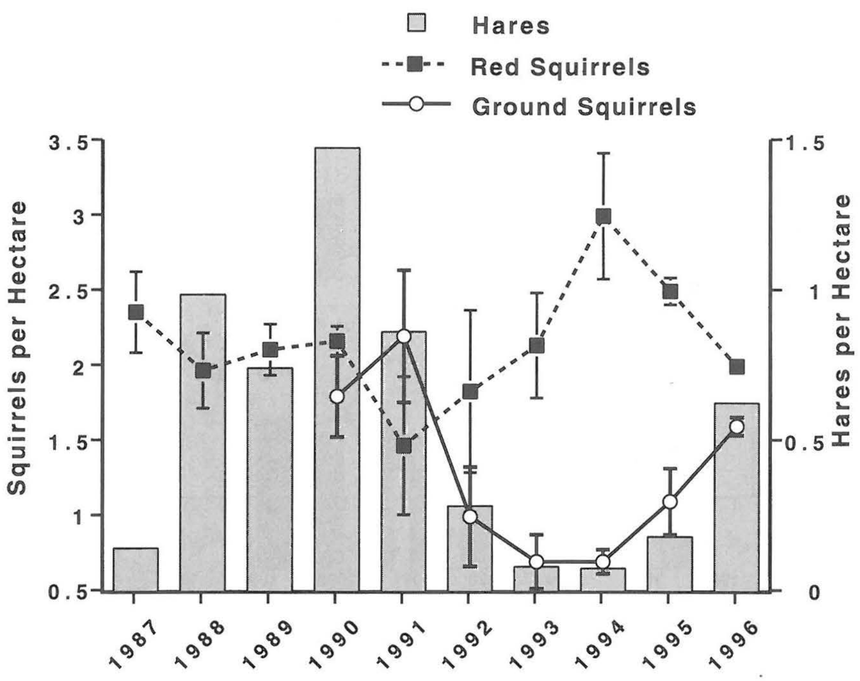

Figure 9.2 Changes in spring abundance of snowshoe hares, arctic ground squirrels, and red squirrels. Ground squirrel estimates from 1990 to 1992 were based on two control areas. Two additional control areas were added in 1993 to increase the precision of our estimates. Red squirrel abundances were averages of three control grids. Error bars (±1 SE) are given for both squirrel species.

To summarize, with one exception (1992, the second summer of the hare decline), adult survival was consistently high. In contrast, juvenile survival from birth to the next spring varied nine-fold from 5% to 45%, and most of this variation occurred in the period between emergence from the nest and the following spring. Recruitment tended to be higher from 1991 to 1995 as compared to 1988–1990.

Reproduction on control areas showed two phases during the study (table 9.1). From 1988 to 1991, less than 70% of the females bred per year, and litter size averaged less than 2.7. Thereafter, the proportion breeding increased to almost 100%, and litter size was well above three. The net result was a substantial increase (two- to threefold) in the number of young produced per hectare in these years. The only exception was 1994, in which the proportion breeding dropped, as did number of young produced per hectare.

Treatment Effects

FOOD ADDITION Red squirrels were frequently observed eating the rabbit chow during both winter and summer. However, it is unlikely that the chow represented high-quality

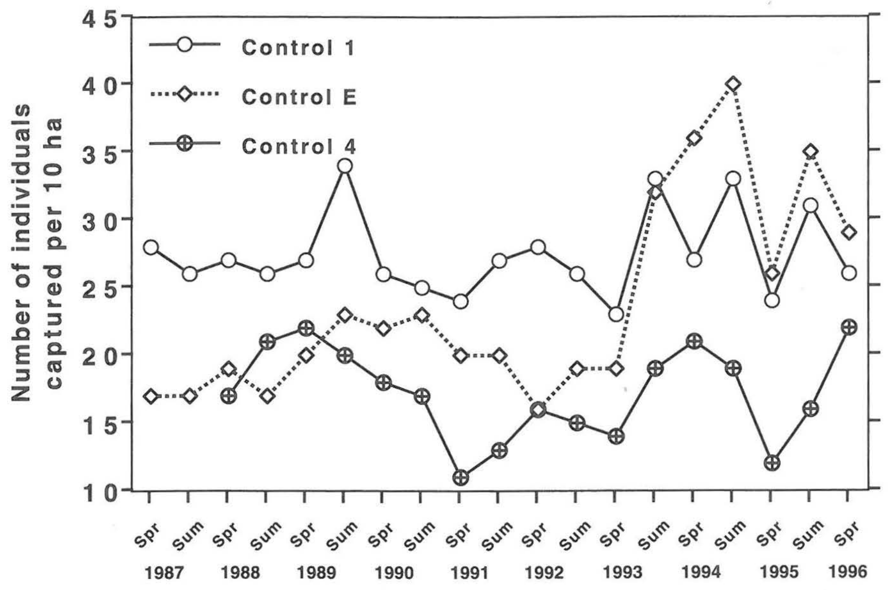

Figure 9.3 Densities per 10 ha of individual red squirrels owning middens on controls 1, 4, and E.

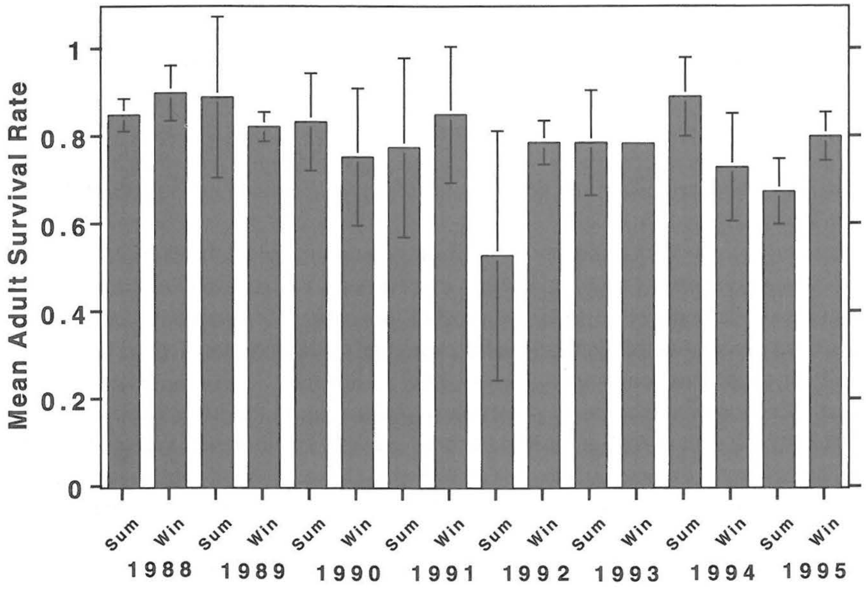

Figure 9.4 Average (95% CLs) 6-month survival of adult red squirrels on controls 1, 4, and E. Summer period covered April through August and winter period covered September through March. Sample sizes of number of individuals followed per grid for each period ranged from 35 to 140 and averaged near 70.

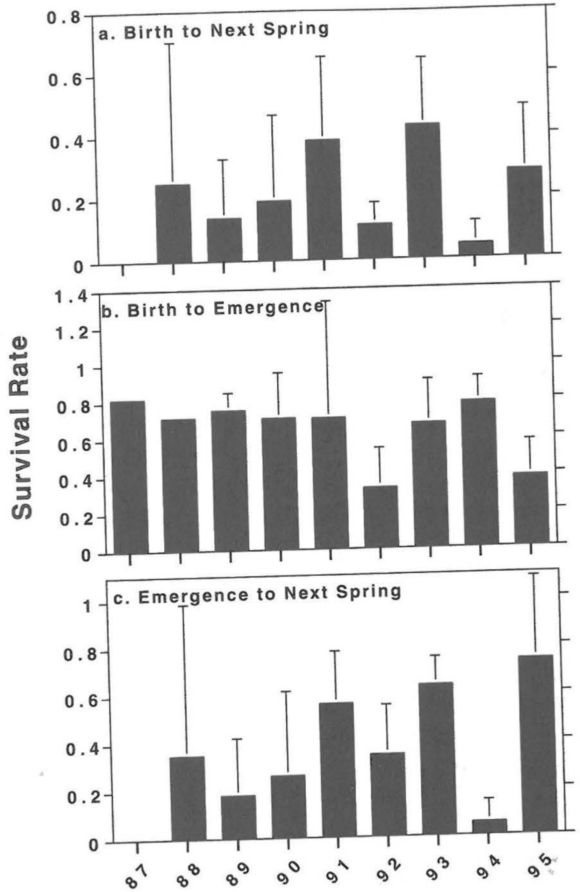

Figure 9.5 Average (95% CLs) survival of young red squirrels on controls 1, 4, and E. Survival is given for three periods: (a) from birth to the next spring; (b) from birth to emergence from the nest (ca. 42 days), and (c) from emergence to the next spring. Sample size of number of young born ranged from 11 to 137 per grid per year and was <30 in only 3 cases.

food given the differences in composition and digestibility of chow compared to conifer seed. The ratio of the number of squirrels on the food grids relative to the control grids was highly variable but tended to be >1 from 1990 onward (figure 9.6). Ratios were never >1.5. As another measure of whether food addition increased squirrel densities, we conducted call surveys on the food grids and adjacent to the grids after spring and summer trapping periods (1991–1995). Calls were counted over a 5-min period on 2 consecutive mornings at each of 16 stations distributed over 35 ha. Call rates on and off of the grids were virtually identical (mean = 7.4 and 8.2 for on vs. off grid), indicating that densities were not higher on the food grids relative to surrounding habitat. Finally, we compared survival of adult squirrels on control and food-supplemented grids over winters following cone crop failures (1989–1990, 1991–1992, and 1994–1995). In all cases, survival

Table 9.1 The average proportion of female red squirrels breeding, the average litter size, and the average number of young produced per hectare on controls 1, 4, and E (sample sizes in parentheses).

Year	% Breeding	Litter Size	Number Produced/ha
1988	55 (80)	2.70 (31)	1.16
1989	67 (99)	2.69 (48)	1.75
1990	39 (104)	2.45 (37)	1.13
1991	65 (100)	2.56 (60)	1.53
1992	81 (162)	3.26 (101)	3.6
1993	82 (150)	3.19 (109)	3.77
1994	66 (173)	3.05 (108)	2.9
1995	98 (134)	3.34 (105)	3.6
1996	93 (122)	3.13 (103)	3.85

on the food supplemented areas was less than that on the control areas (table 9.2; sample sizes of 16–36 on the three food-supplemented grids: food 1, food 2, and predator exclosure + food). Thus, addition of rabbit chow had no positive effect on red squirrel numbers or survival.

PREDATOR EXCLUSION Exclusion of predators did not lead to higher squirrel densities. Figure 9.6 shows that the density ratio on the predator exclosure was always <1, and it remained constant over the course of the hare cycle. We hypothesized that predation would have its greatest impact on squirrels when snowshoe hares had declined and the predators would be forced to consume alternate prey (1991–1993). As a test, we intensified our efforts on the predator exclosure just before and during the hare decline. Survival rates of adults were significantly higher on the predator exclosure than on the control grids in the winter of 1991–1992 and summer of 1992, but not in summer of 1993 (table 9.2; Stuart-Smith and Boutin 1995). In the summer of 1992, all mortalities were a result of predation (Stuart-Smith and Boutin 1995). The predator exclosure eliminated only large mammalian predators, which suggests that mammalian predators had a short-term impact on adult survival during the hare decline. The particularly poor survival of juveniles from birth to emergence in 1992 (figure 9.5) may in part have been due to death of their mothers in that period (figure 9.4). However, this poor survival did not carry over into the period after emergence, as survival from emergence to the following spring was average. Thus, predator-induced low survival rates in both adults and young were short-lived, and the impact on the red squirrel populations had little long-term effect.

INTERACTIVE EFFECTS OF FOOD AND PREDATION Given the results of the food addition and predator exclosure treatments, we did not expect to see any effect of the combined treatment on red squirrel densities. The density ratios on this treatment were almost always <1 (figure 9.6), and survival on the predator exclosure + food grid was never substantially greater than that observed on the control areas (table 9.2).

FERTILIZATION We do not think that the fertilizer treatment had any direct relevance to red squirrels. The only potential effect may have been on cone crop, and the fertilizer had

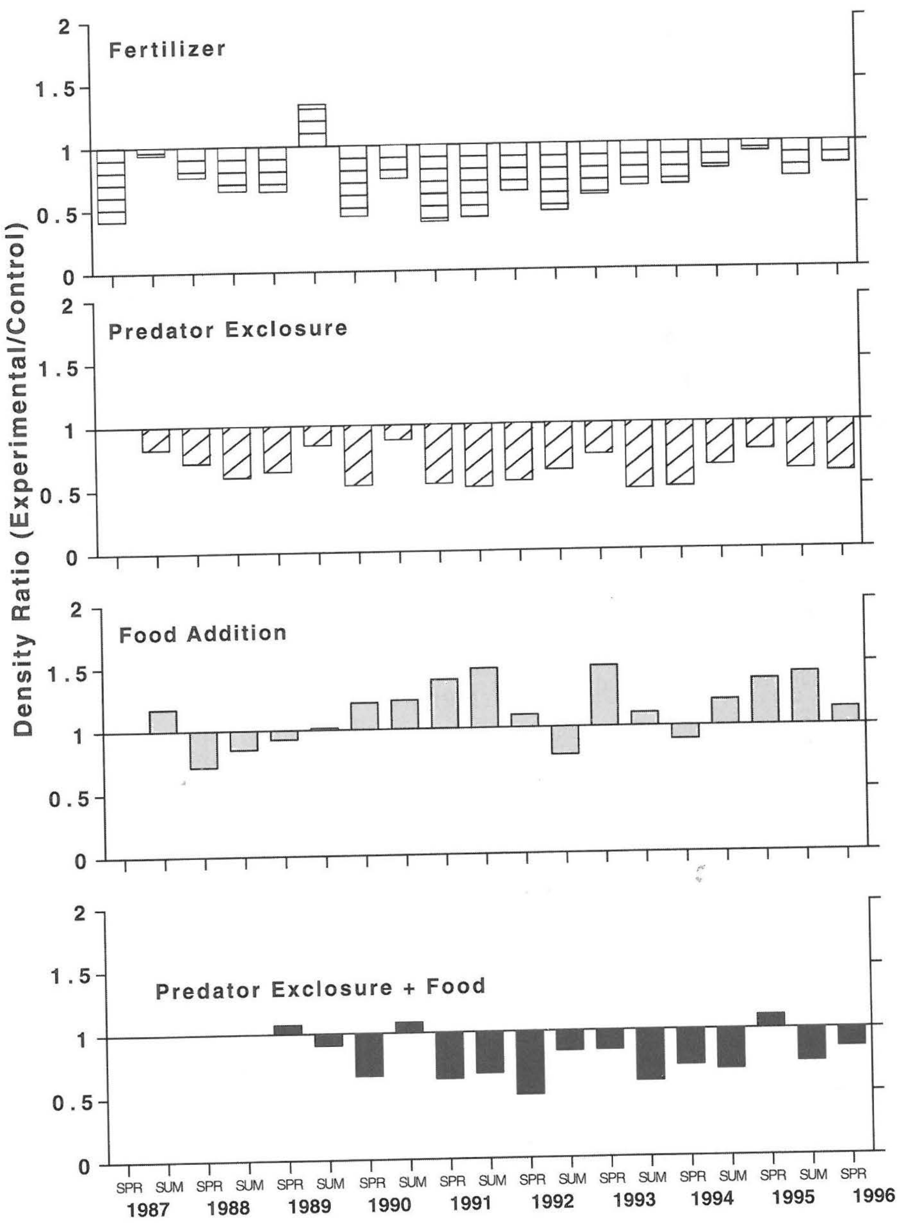

Figure 9.6 Ratios of treatment densities to average control population densities of red squirrels. Ratios of 1 indicate no difference with control densities. Control densities as in figure 9.2. Values for the fertilizer and food-addition grids were averages of two grids in each case.

Table 9.2 Six-month winter survival rates (2 SE) for red squirrel adults on control and experimental grids.

Grid	1989–90	1990–91	1991–92	1992–93	1993–94	1994–95
Control	0.84 (0.02)	0.79 (0.06)	0.87 (0.06)	0.89 (0.08)	0.82 (0.01)	0.77 (0.06)
Food addition	0.77 (0.16)	0.76 (0.13)	0.74 (0.18)	0.88 (0.12)	0.91 (0.08)	0.66 (0.08)
Predator exclosure	0.63	0.42	0.96	0.82	0.84	0.67
Predator exclosure + food	0.72	0.83	0.70	0.71	0.79	0.68

Rates were calculated as the proportion of individuals caught during summer or autumn that were recaptured the following May. Time periods between sessions varied from 24 to 42 weeks. All rates were standardized to a 6-month period.

no effect on this (see figure 7.7). We monitored fertilizer 1 intensively from 1987 through 1993. The changes in numbers on this grid are notable, as they were the most drastic of any of the sites studied. Numbers dropped almost threefold between autumn 1989 and spring 1990. They remained low through the early 1990s before recovering in 1993. The decline in 1989–1990 is even more drastic when survival rates are examined. Only 15% ($n = 60$) of the adults and 0% of the juveniles ($n = 27$) survived that winter. We regularly found mummified carcasses of squirrels in nests while we were searching for young in the spring of 1990. It appears that most of the mortality was due to starvation. Fertilizer 1 appeared to represent low-quality habitat. It was the driest site, and cone crops on this area were the lowest of all the study sites.

Role of Stochastic Factors Squirrels rely heavily on conifer seed, which is highly variable from year to year. All study grids showed similar year-to-year patterns, but the average number of cones per tree varied between sites. Over the course of the study, there were cone failures in 1989, 1991, and 1994, above-average cone years in 1992 and 1995, and a mast year in 1993 (see 7.1.3 for details). We have limited data for years before 1987, but 1983 was a mast year and 1985 and 1986 were average or above average. We hypothesized that changes in density would be related to cone availability. To test this idea, we standardized squirrel numbers caught on all grids by calculating standardized deviates for each grid and compared this with our cone index. The cone index was significantly correlated with the standardized deviate of the number of squirrels caught in the following spring ($r = .48, p < .0001, n = 78$) and autumn ($r = .55, p < .0001, n = 68$; figure 9.7). Similarly, finite population growth from spring to spring was related to cone crop. When the cone index was <10 per tree, populations increased in only 8 of 29 cases, whereas when it was >10 per tree, numbers increased in 26 of 34 cases.

We also examined the survival rates of squirrels in relation to cone supply and predicted low overwinter survival in years of cone failure. This prediction was not supported for adults, as survival was only slightly lower in one (1994–1995) of the 3 years of cone failure. The lowest survival rates occurred in summer 1992, which followed the cone crop failure of 1991. However, similar failures in 1989 and 1994 did not result in low survival the next summer (1990 and 1995, respectively). Thus, it is unlikely that the absence of cones from the previous autumn has anything to do with poor adult survival in the following summer. Juvenile survival did not show any clear relation to cone crop. Survival from birth to emergence (figure 9.5b) was low in 2 of the 3 years following a cone failure. The summer of 1990 was the exception. Survival from emergence to spring was both low (<10% in 1994) and high (>50% in 1991) in years of cone failure (figure 9.5c).

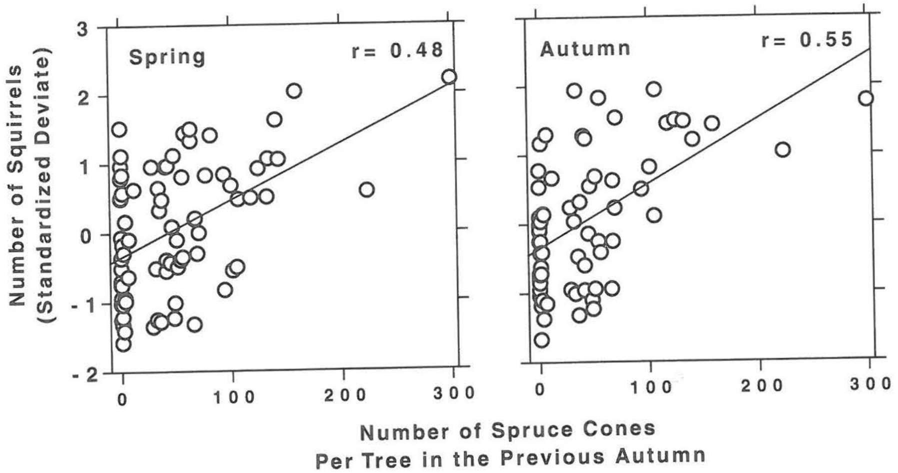

Figure 9.7 The relationship between the production of spruce cones per tree on trapping grids in late summer and the standardized deviate of red squirrel numbers on these trapping grids in the following spring and the following autumn.

Finally, production of juveniles appeared to be related to the cone crop in the current year rather than to that in the preceding year. This is surprising given that all young are conceived before the current year's cone crop appearing on the trees. Table 9.1 shows that juvenile production doubled in 1992, a year that followed a cone failure but preceded a mast year. Production declined somewhat in 1994 even though the previous year was a mast year. Adult females appear to anticipate (possibly through consumption of cone buds that are produced in the previous summer and are available to squirrels during the winter before a mast crop) and adjust their investment accordingly.

9.4.2 *Arctic Ground Squirrels*

Population Demography on Control Sites Spring populations from 1990 to 1996 fluctuated in close synchrony with that of the snowshoe hares populations ($r = .89, n = 7$; figure 9.2). Ground squirrels were still increasing from 1990 to 1991, reaching an average of 2.2/ha in 1991, but as hares rapidly declined from 1991 to 1992, finite rates of increase for squirrels dropped to <0.5 (figure 9.8). Ground squirrel populations declined 54% by spring 1992 and another 30% by spring 1993, to reach constant levels of 0.7/ha from 1993 to 1994. When hare populations started increasing in the summer of 1994 (chapter 8), so did ground squirrels, with some controls doubling their numbers each year (finite rates of increase of 2; figure 9.8).

From 1990 to 1993, survival of adult ground squirrels declined as total snowshoe hare biomass declined (figure 9.9a, c). Hubbs and Boonstra (1997) calculated an index of survival of adult squirrels on controls based on trapping records and showed that survival

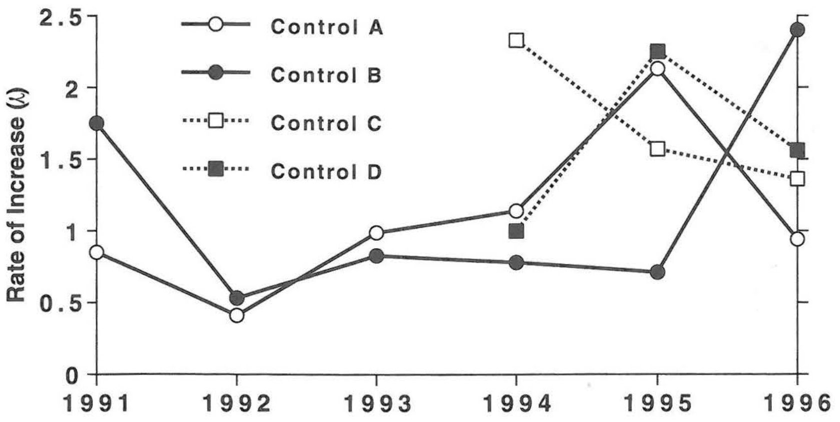

Figure 9.8 Finite rates of increase (λ) of ground squirrel populations on each of the control sites monitored from 1990 to 1996. The value for each year represents the rate of change in abundance from the previous year.

over the 3-month active season declined by more than half from 70% in 1991 to 31% in 1992 (table 2 in Hubbs and Bonstra 1997). Survival estimates from trapping records underestimate survival by 35–39% but still provide a comparable relative index of survival (Hubbs and Boonstra 1997). Further estimates of survival based on radio telemetry showed that adult ground squirrel survival increased markedly from a 3-month survival of 36% in 1993 to 91% in 1994 (table 9.2), when both total mammalian predator and total avian predator biomass were lowest (figure 9.9b).

During the active season, predation was the greatest proximate cause of mortality of both radio-collared juveniles and adults from 1992 to 1995. Of the adults radio collared from 1992 to 1995 and juveniles radio collared from 1993 to 1995, predation accounted

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Figure 9.9 (a) Total biomass (kg/ha) for snowshoe hares (1989–1995) and for arctic ground squirrels (1990–1995) on control areas. Methods for estimating snowshoe hare density and biomass are described in chapter 8. Biomass for ground squirrels was calculated by multiplying the average weight of a ground squirrel (0.47 kg) by population density. (b) Total biomass for mammalian predators (lynx and coyotes; kg/350 km^2) and for avian predators (great horned owls, red-tailed hawks, and goshawks; kg/100 km^2) from 1989 to 1995. Methods for estimating mammalian predator densities and biomass are described in chapter 13. Methods for estimating avian predator densities and biomass are described in chapter 15. (c) Twenty-eight-day summer season survival and overwinter survival of adult and juvenile ground squirrels on control sites. Summer survival of juvenile ground squirrels was measured from 1993 to 1995. Active season survival in 1990 and 1991 was estimated from trapping data and in 1992 from radio telemetry collected by Hubbs and Boonstra (1997). Overwinter survival in females was recorded from trapping records obtained in late autumn and early spring. (d) Litter sizes and weaning rates of adult female ground squirrels on control sites. Litter size was measured from 1991 to 1995. Weaning rate, which is the percentage of female ground squirrels that were successful in weaning a litter, was measured from 1993 to 1995.

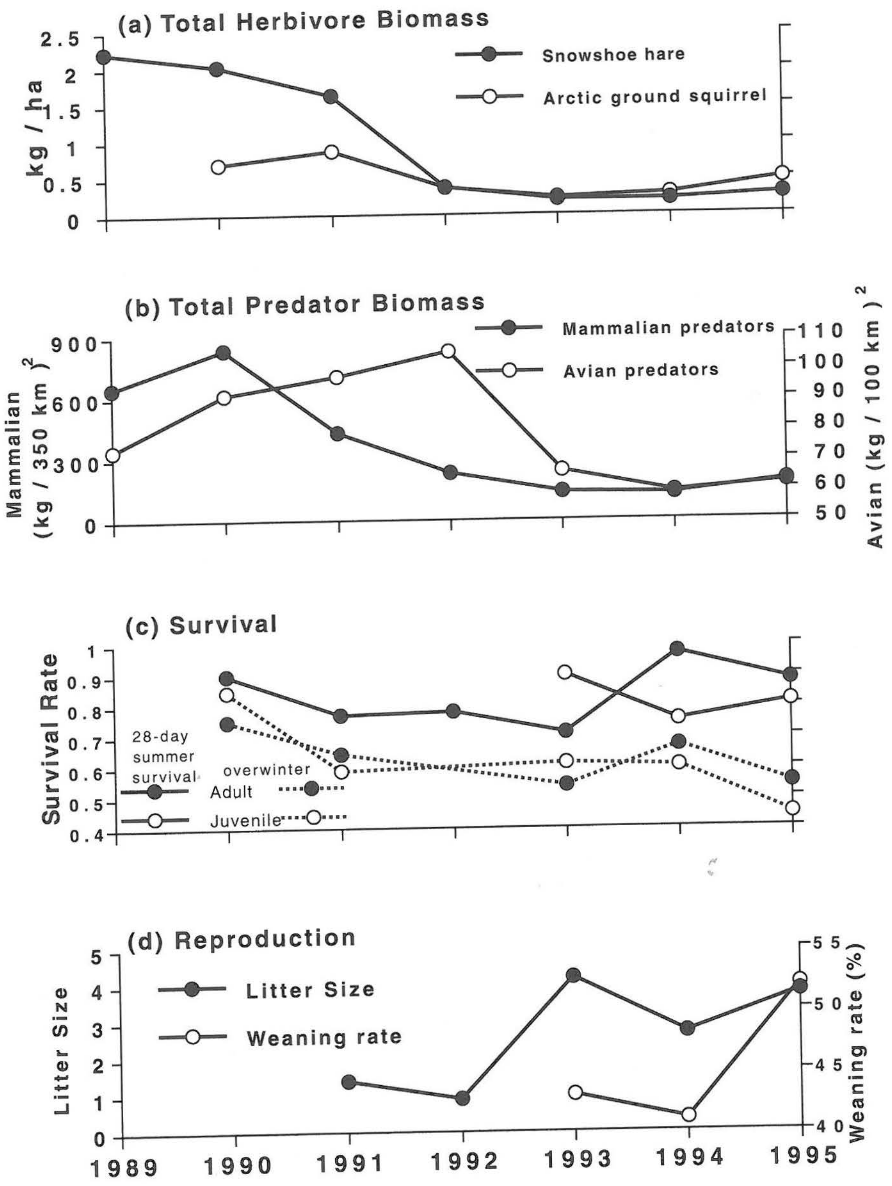

Figure 9.9

for 96% (73 of 76) and 96% (52 of 54), respectively. During the second year of the hare decline (1992), avian predators accounted for 62% of known predator kills (Hubbs and Boonstra 1997). From 1993 to 1995, when snowshoe hare densities (figure 9.2) and total biomass (figure 9.9a) were at their lowest, and avian predator biomass at its highest (figure 9.9b), avian predators accounted for most of the known kills (75% of adults, $N = 24$ and 79% of juveniles, $N = 31$) of known predators.

Overwinter survival of adult and juvenile females was determined from trapping data (1990–1996). We present only overwinter survival of females (figure 9.9c), as it is difficult to separate dispersal from overwinter mortality in males because we were not present when possible dispersal could have occurred from late September to October before hibernation or from late March–April just after hibernation. Overwinter survival averaged 63% ($N = 72$) for juvenile females and 61% ($N = 72$) for adult females from 1990 to 1996. Survival of both age classes combined was greatest during the winter of 1990–1991 (81%, $N = 21$), declined to approximately 60% and remained at this level until the winter of 1995–1996 when survival decreased to 52% ($N = 31$).

Reproduction on control sites (figure 9.9d) varied considerably from 1991 to 1995. Recruited litter sizes were small during 1991 and 1992 (approximately 1.2 pups per litter) when predators were numerous and hares declining (figure 9.9b). When hares and predators were at low densities from 1993 to 1995, litter sizes for ground squirrels tripled to an average of 3.6 pups per litter. We only measured weaning rate from 1993 to 1995 (figure 9.9d). During this period from 42% to 51% of females weaned litters.

Treatment Effects on Demography

DENSITY Our experimental treatments had major effects on ground squirrel populations, and, to assess the impact of the treatments, we present the changes relative to those occurring on the control grids (figure 9.10). The fertilizer addition had a progressively negative effect on squirrel densities. Densities were either similar to (fertilizer 2) or higher (fertilizer 1) than those on controls in 1990, but thereafter (1992–1996), they averaged only 40% of that on controls (figure 9.10). Fertilizer 2 declined to such an extent that ground squirrels were absent during the last 2 years of the project. On the predator exclosure spring population densities averaged 1.9 times those of controls (average spring density over the study was 3.2/ha) and reached a maximum of 2.6 times control densities by spring of 1995. The doubling of density on the predator exclosure was already evident by 1991, but the population was not able to sustain this and declined drastically from 1991 to 1992 when hares were declining. This treatment may have converged back to control levels as a result of great horned owls, which continued to increase until 1992 (chapter 15), and these were not excluded from the predator exclosure. However, we were not able to detect any difference from control levels in mortality during this period (either during the active season or overwinter). After 1992 densities again reached values more than double control levels (figure 9.10).

On the two food grids, densities averaged five times that of the controls, and there was little change over time (spring densities averaged 6.1/ha on the food 1 and 3.4/ha on food 2 over the study, reaching a maximum of 7.3 times on food 1 during the spring of 1996 [figure 9.10]). Food 1 and food 2 fluctuated together during 1993 and 1994 but increased loss due to overwinter mortality on food 2 during the winter of 1994/1995 caused them to diverge. On the predator exclosure + food grid densities averaged 10.8 times that of controls and diverged progressively from 1991 to 1996, reaching a maximum spring density of 31/ha in the spring of 1996 (19 times that of controls). Thus, whereas the effect of nutrient addition was clearly negative, the exclusion of predators was positive (2-fold increase over control levels), the addition of food was positive (5-fold increase), and, when the treatments were combined, they had a multiplicative effect (11-fold increase on the predator exclosure + food).

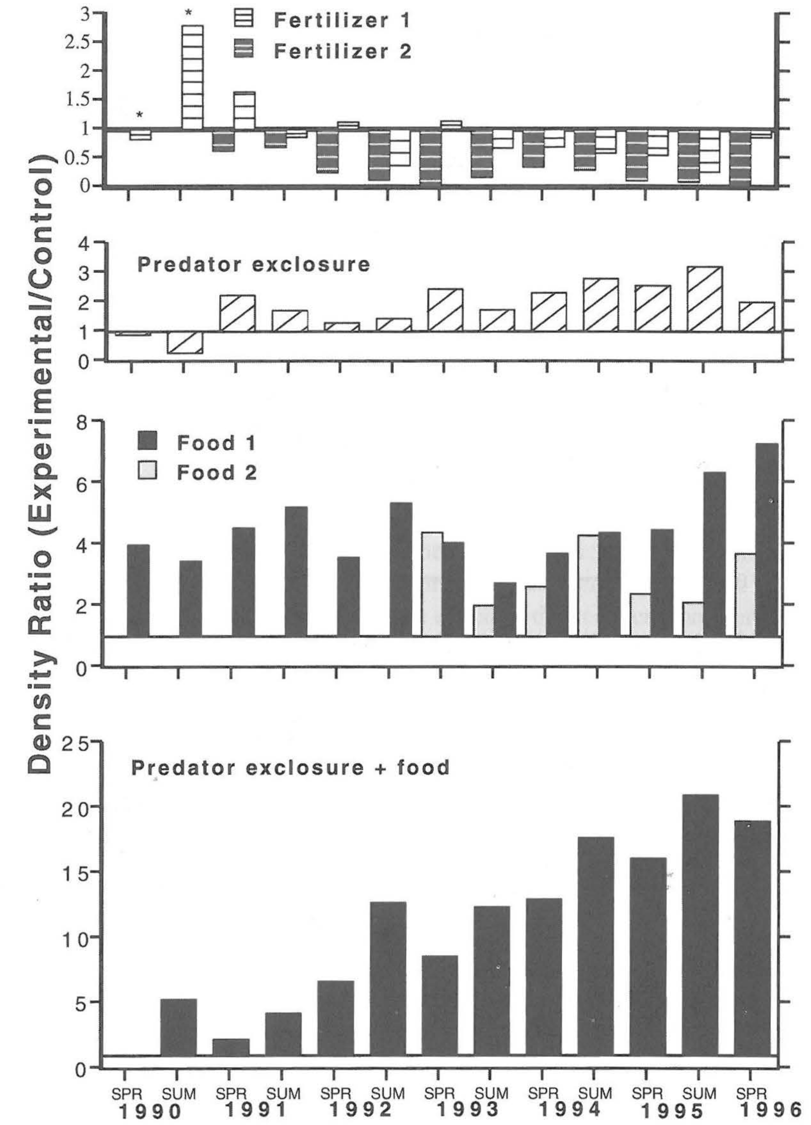

Figure 9.10 Ratios of treatment densities to average control population densities of arctic ground squirrels. Ratios of 1 indicate no difference with control densities. Control densities as in figure 9.9a. *Minimum number alive used for 1990 density on fertilizer treatment.

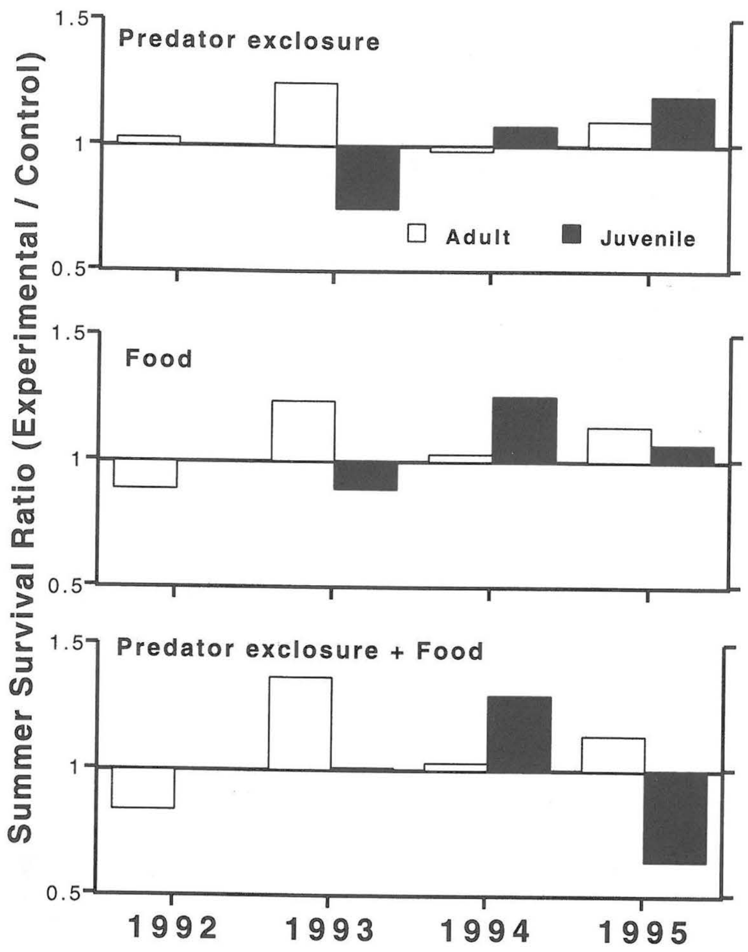

Figure 9.11 Ratios of treatment summer survival to average control survival for adult (1992–1995) and juvenile (1993–1995) arctic ground squirrels. Values >1 represent positive treatment effects (i.e., increased survival relative to controls); values <1 represent negative treatment effects (lower survival relative to controls).

SURVIVAL Active season survival of radio-collared adults or juveniles was unaffected by the experimental treatments from 1992 to 1995 (figure 9.11; (adults: $\chi^2 = 5.88$, df = 3, $p \geq .21$ for all years, juveniles: $\chi^2 = 6.25$, df =3, $p \geq .10$ for all years). Survival of both adults (1992–1995) and juveniles (1993–1995) was affected by year (adults: $\chi^2 = 159$, df = 3, $p < .0001$; juveniles: $\chi^2 = 5.6$, df = 2, $p = .06$). Thus, changes in survival on the controls from one year to the next were reflected by similar changes in survival on the treatments. Average juvenile 28-day survival over 1993–1995 ranged from 2% to 14% lower than the survival of adults on the experimental treatments (table 9.3).

Overwinter survival, calculated from trapping records, averaged 74% ($N = 903$) over all treatments and years. Both year and treatment were significant in explaining overwinter survival of ground squirrels. However, their effect was interactive (logistic regression: $\chi^2 = 28$, df = 12, $p = .006$), meaning that the effects of the treatments on overwinter survival changed from year to year. Squirrels on food-supplemented grids had worse survival than controls in the winters of 1991–1992 and 1992–1993, but better survival than controls from 1993 to 1995 (figure 9.12). Predator exclusion had no consistent effect on the overwinter survival of females (figure 9.12). High overwinter survival from 1993 to 1995 was echoed by our estimates obtained using radio-collared females. Overwinter survival from 1993 to 1996 (all treatments combined for radio-collared females) was 97% (92 of 97 individuals). Comparisons among treatments or years were not possible because so few died.

Table 9.3 Twenty-eight-day active season survival (with 95% confidence limits) of radio-collared adult and juvenile ground squirrels on experimental sites and controls from 1992 to 1995.

	Year	Controls	Predator Exclosure	Food	Predator Exclosure + Food
Adults	1992	0.79 (0.74–0.83)	0.81 (0.76–0.87)	0.70 (0.66–0.74)	0.66 (0.61–0.71)
	1993	0.71 (0–0.92)	0.89 (0.78–0.97)	0.88 (0.77–0.96)	0.97 (0.94–1.0)
	1994	0.97 (0.92–1.0)	0.95 (0.85–1.0)	1	1
	1995	0.88 (0.73–0.98)	0.97 (0.93–1.0)	1	1
	All	0.84 (0.59–1.0)	0.90 (0.71–1.0)	0.90 (0.82–0.97)	0.91 (0.86–0.95)
Juveniles	1993	0.91 (0.71–1.0)	0.68 (0.42–0.83)	0.81 (0.63–0.94)	0.92 (0.74–1.0)
	1994	0.74 (0.47–0.91)	0.80 (0.62–0.93)	0.93 (0.85–1.0)	0.96 (0.87–1.0)
	1995	0.81 (0.58–0.97)	0.97 (0.9–1.0)	0.87 (0.73–0.98)	0.52 (0–0.76)
	All	0.82 (0.48–0.9)	0.80 (0.58–0.87)	0.87 (0.76–0.93)	0.77 (0–0.88)

REPRODUCTION The size of litters at emergence showed the same pattern of variation on both controls and treatments from 1991 to 1995, with 1992 having the smallest litter sizes (figure 9.13). However, litters were larger on all treatments in at least 4 of the 5 years, but when pooled, treatment effects were not significant (figure 9.13). Thus, these differences were not sufficient to explain the differences in density among treatments.

Weaning success differed markedly among controls and treatments. For the period from 1993 to 1995, we examined the proportion of females that were successful in weaning a litter by logistic regression (year × treatment). Weaning success was significantly better on the treatments, but the effect was not independent of the effect of year (interaction effect: 21.3, df = 11, $p = .03$). Weaning success (figure 9.14) varied as follows: predator exclosure + food (83%) > food (77%) > predator exclosure (72%) > controls (45%). Thus, the presence of food or the absence of predators had a similar effect and increased the weaning rate by 60% over control levels.

First emergence of young from the natal burrow was strongly affected by the food addition. Because estrus occurs within 3–4 days of emergence, and both gestation and the length of time the young spend in the burrow are constant (25 days and 27 days, respec-

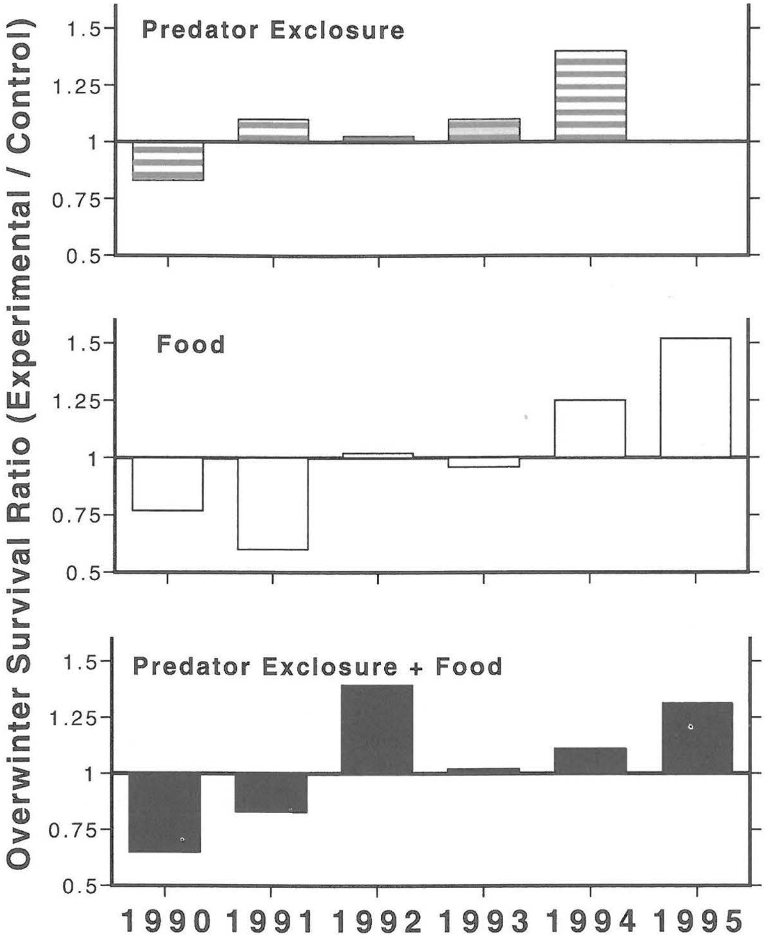

Figure 9.12 Ratios of treatment overwinter survival to average control survival for adult female arctic ground squirrels (1990–1995). Values >1 represent positive treatment effects (i.e., increased survival relative to controls); values <1 represent negative treatment effects (lower survival relative to controls).

tively; Lacey 1991), earlier appearance of the young must mean earlier breeding. Thus the young have a longer period of time to grow before hibernation. On the controls and on the predator exclosure, emergence date ranged from June 13 to June 23 for all years except 1992 (table 9.4). Severe spring weather in 1992 delayed breeding, and hence juvenile emergence occurred in early July, about 3 weeks later than normal. On the food grids (including the predator exclosure + food), emergence was generally 1–2 weeks earlier than in control areas, even in 1992. Thus, food addition permitted earlier initiation and completion of reproduction.

WEIGHT DYNAMICS Body mass of females just after emergence from hibernation is critical for reproductive success. We examined how our treatments affected body mass with a two-way ANOVA (treatment × year; figure 9.15). All variables were significant (treatment: $F = 74.0$, df = 3, $p < .0001$; year: $F = 8.6$, df = 6, $p < .0001$; interaction: $F = 4.6$, df = 18, $p < .0001$). Body mass was lower on all sites during the spring of 1992 (figure 9.15) when weather conditions were poor, and this contributed to the year effect. There was overlap in body mass between food-addition grids and non–food-addition grids in some years, which accounts for the interaction effect that we detected. Spring female body mass over the entire study was ranked as follows: predator exclosure + food = food > predator exclosure > controls. Average spring body mass was found to be positively correlated with average litter size produced by the females that year ($r = .51$, $N = 5$ years) and average weaning success ($r = .68$, $N = 3$).

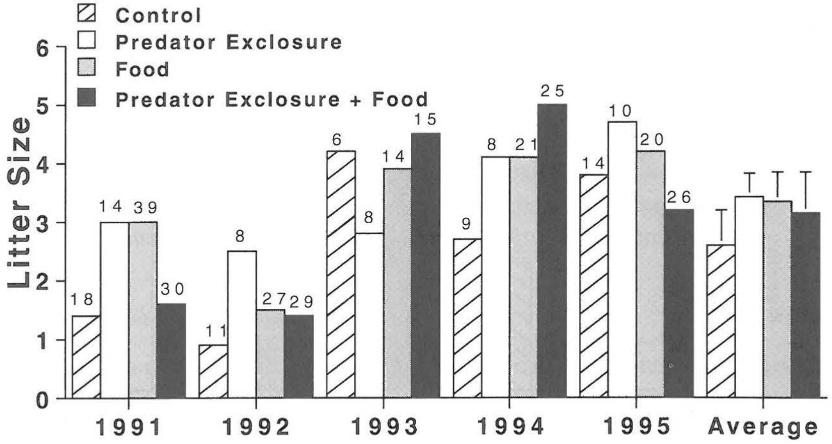

Figure 9.13 Litter sizes for arctic ground squirrels on treatments and controls (1991–1995). Sample size for adult females is indicated above bar. Average litter sizes (all years pooled) are shown with SEs.

9.5 Discussion

The responses of the two squirrel species, red squirrels and arctic ground squirrels, are at two ends of the spectrum. Red squirrel populations showed virtually no response to the snowshoe hare cycle, modest responses to the fluctuations in the cone crop, and virtually

Table 9.4 Earliest date of juvenile arctic ground squirrel emergence from natal burrows for treatment and control areas, 1991–1995.

Treatment	1991	1992	1993	1994	1995
Controls	21 June	4 July	14 June	13 June	20 June
Predator exclosure	23 June	5 July	18 June	13 June	20 June
Food	17 June	26 June	14 June	6 June	5 June
Predator exclosure + food	13 June	27 June	7 June	6 June	6 June

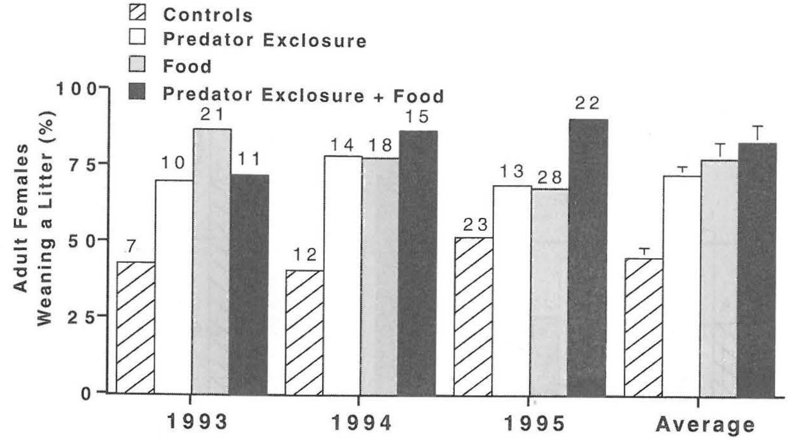

Figure 9.14 Weaning rate for arctic ground squirrels on treatments and controls (1993–1995). Weaning rate is the percentage of females that successfully wean their litter. Average weaning rates (all years pooled) are shown with SEs.

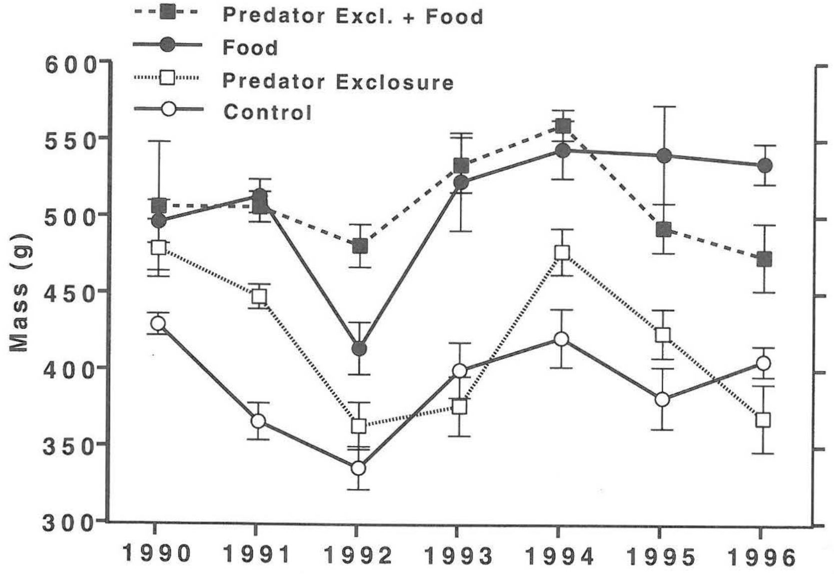

Figure 9.15 Average spring body mass (± SE) of adult female arctic ground squirrels on treatments and controls from 1990 to 1996.

no response to any of the experimental treatments. In contrast, arctic ground squirrels fluctuated in tandem with the snowshoe hare cycle, showed dramatic responses to changes in food supply (both positive [food addition treatments] and negative [fertilizer addition treatment]) and to removal of predators. Thus, in the boreal forest ecosystem of the southern Yukon, red squirrel populations are characterized by constancy and arctic ground squirrel populations by long-term fluctuations. We examine the pattern first with respect to changes in demography relative to the snowshoe hare cycle and to stochastic changes in the environment and then in relation to the experimental treatments.

9.5.1 Role of Stochastic Events

Populations rarely remain constant over time because short-term environmental stochasticity, particularly acting though weather, can affect such factors as food supply (Sinclair and Pech 1996), which then affect the population demography. We found that the size of the spruce cone crop was a good predictor of red squirrel population growth and density the next spring and autumn. This begs the question of the causes of the fluctuations in the cone crop. In the deciduous forests of Europe, outbreaks of microtines are directly related to mast production by the major seed-producing trees, and these mast years are directly related to weather patterns of the previous year (Pucek et al. 1993). In red squirrel populations of Alberta, Kemp and Keith (1970) found that drier summers one year produced larger cone crops or mast years the next. When we examined correlations between temperature and precipitation from May to August of one year, (chapter 2; months examined individually or summation of these months) and the size of the spruce seed crop the next year ($N = 8$), no correlation was significant (the highest was the average May temperature, $r = -.64, p = .09$). Thus, the peak spruce cone and seed mast year of 1993 (chapter 7, figure 10.4), the highest in our 10-year study, appeared unrelated to delayed weather patterns in any obvious way, and some other explanation must account for this mast year. Both this peak mast year and the previous one (1983) followed the peak of the snowshoe hare cycle by about 3 years, and in the nutrient section below, we suggest that this may not simply be chance.

Variation in weather can have major effects on ground squirrel populations. Though the annual cycle of hibernation and activity in ground squirrels is an endogenous, circannual one (Blake 1972, Davis 1976), timing of emergence and reproduction may be controlled by exogenous factors linked to weather (Morton 1975, Davis 1976). Delayed snow melt in spring reduces the availability of food, causing ground squirrels to rely more on their remaining fat reserves, thereby affecting their survival and reproduction. Ground squirrels depend heavily on remaining fat reserves for reproduction after hibernation, but those remaining fat reserves are insufficient without available forage to support a litter to weaning (Kiell and Millar 1980). Michener and Michener (1977) found that Columbian ground squirrels (*S. columbianus*) and Richardson's ground squirrels (*S. richardsonii*) emerged from hibernation 12 and 21 days earlier, respectively, during a warm spring than during a cool one. After a particularly severe and long winter, Phillips (1984) found pregnancy loss in golden-mantled ground squirrels (*S. saturatus*). After a month-long snow storm in spring, Morton and Sherman (1978) reported poor survival, delayed breeding, and reduced reproduction in Belding's ground squirrels (*S. beldingi*). Finally, after a drought and a prolonged winter, Van Horne et al. (1997) reported lower adult survival, delayed emergence and reproduction, and low mass and complete loss of juveniles in Townsend's ground squirrels (*S. townsendii*).

In our study, 1992 had a delayed spring in which snow cover persisted for almost 3 weeks longer than normal, and this was associated with major population declines in all populations (Hubbs and Boonstra 1997). Overwinter survival dropped from an average of 74% in all other years to 50% during the winter of 1991–1992. Reproduction was delayed by 17–19 days across all treatments and controls as indicated by timing of juvenile emergence (table 9.4). Combined with small litter sizes during 1992 (figures 9.9d, 9.13), these effects may have also contributed to the further decline in ground squirrel densities on control sites from 1992 to 1993 (figure 9.2). Food addition ameliorated the severity of this spring only on the predator exclosure + food grid, where we could deliver the food by hand in spite of the snow. Food addition was not effective on the food-addition grid at that time because of food consumption by grizzly bears and moose (Hubbs and Boonstra 1997). This severe spring was coupled to intense predator pressure during 1992 and served to converge all the trapping areas more than they otherwise might have been.

9.5.2 Treatment Effects

Role of Nutrients The boreal forest is a nutrient-limited environment, and we had expected that the addition of fertilizer would increase squirrel densities by stimulating plant productivity (spruce seed production in the case of red squirrels; herbs and grasses in the case of ground squirrels). Spruce seeds increased slightly, and perennial graminoides (*Festuca altaica* and *Calamagrostis lapponica*) and two herbs (*Epilobium angustifolium* and *Achillea millefolium*) (Nams 1993) increased markedly, but legumes did not (chapter 5, John and Turkington 1995). Both squirrel species decreased markedly. Why? Red squirrels may have declined because of the negative effects of fertilization on mushroom crops (S. Boutin personal observation), an alternative food which is readily harvested and stored (M. C. Smith 1968) and which may be one of the few food sources if the cone crop fails. However, our evidence for this is weak. Thus, intensive fertilization such as we applied on the fertilizer treatments may be partly responsible for the red squirrel decline. However, three lines of evidence suggest that widespread, low-level fertilization related to nutrient release associated with the hare peak (decaying hare pellets produced at the hare peak and possibly decaying vegetation clipped from shrubs at the peak) may affect red squirrel populations through its affects on the cone crop. First, our biggest mast year, 1993, was not related in any obvious way to weather patterns and followed the hare peak by about 3 years. Another mast year, 1983, followed the hare peak by about 3 years. Second, peaks in northern red-backed voles also occurred about 2–3 years after the hare peak (chapter 10). Third, shrub biomass reached its highest level at the peak (1990) and in the next 2 years (see figures 6.2, 6.5).

Ground squirrels may have declined because certain plants (and the essential chemicals they contain) critical to successful hibernation largely disappeared with the addition of fertilizer. Addition of fertilizer shifted the competitive balance from those plant species that grow well in a nutrient-limited environment (particularly the nitrogen fixers such as the lupines) to those that grow well in a nutrient-sufficient environment (particularly the grasses, chapter 5, Turkington et al. 1998). For successful hibernation, ground squirrels require a diet high in polyunsaturated fatty acids (Geiser and Kenagy 1987, 1991, Frank 1992, 1994). Legumes (such as lupines and vetches) are good sources of these fatty acids; grasses are not (Harwood and Geyer 1964, Lehninger 1982). Polyunsaturated fatty acids lower the melting point of depot fats (Mead et al. 1986), increasing the proportion of individuals capable of hibernating, increasing torpor bout duration, and decreasing body temperature during hibernation. Thus, our evidence suggests that ground squirrels declined markedly because they were not able to hibernate successfully on the fertilized grids. The corollary of this is that ground squirrels would not be able to inhabit the boreal forest if it were not nutrient limited.

Role of Food Red squirrel populations were relatively constant over time in the face of major changes in two key factors, cone supply and predation pressure. Although local areas experienced changes in numbers as great as fourfold, average numbers remained remarkably constant. Cone availability seemed more important than predation in causing year-to-year changes. It was only when cones were scarce (cone crop failure in 1991) and predation pressure near its maximum (summer 1992) that predation seemed to have any noticeable effect on survival. Despite low adult and early juvenile survival, populations on many areas increased from 1992 to 1993. This was due to a substantial increase in litter size, in the proportion of females breeding, and in the number of multiple litter attempts in that year. Females anticipated the abundant cone crops of 1992 and 1993 by increasing their reproductive effort. This anticipatory reproductive response was first observed by Svärdson (1957), who proposed that increases in clutch size of Finnish game birds in years of peak seed production was a consequence of the peak in nutritionally superior reproductive buds the previous winter. This phenomenon has also been observed in a number of red squirrel studies (C. C. Smith 1968, Kemp and Keith 1970). The ability of squirrels to cache food and use it over multiple years tends to smooth out the major fluctuations in cone supply. Individuals that acquire a territory are capable of surviving complete cone failures.

Although cone availability provided a reasonable explanation for some of the red squirrel dynamics observed, there were some perplexing inconsistencies. Juvenile survival to emergence was low in two of the three summers following a cone failure in the previous autumn. The exception to this pattern occurred in 1990, the summer of maximum hare numbers. Our research on survival of leverets (chapter 8) indicated that squirrels were killing baby hares at a high rate during this period (O'Donoghue 1994). Relatively few female squirrels bred that year, but those who did may have been able to get enough energy from eating baby hares to keep their offspring alive to emergence. Similarly, survival from emergence to the next spring was good in 1991–1992 (the winter of hare decline) despite the cone crop failure of 1991. This high survival may have been due to squirrels scavenging hares that had been killed and cached by predators.

Though both species ate the rabbit chow on the food-supplementation grids, rabbit chow had no effect on the demography of red squirrels but marked effects on that of the arctic ground squirrels, and thus we only address its effects on the latter. Food addition played a greater role in the population dynamics of ground squirrels than did predation. Increases in density on food-addition treatments averaged fivefold over control densities, twice that of the predator exclosure. The typical response to food addition in vertebrate populations has been a doubling of density, but few studies have supplied food for more than one year (Boutin 1990). In Columbian ground squirrels (*S. columbianus*), Dobson and Kjelgaard (1985) supplemented two populations at different elevations over a 2-year period, resulting in a 1.5–2.3 increase in density. One of the problems with short-term food-addition studies is that they do not incorporate possible pretreatment maternal effects (Bernardo 1996) that may reduce the response to the experimental manipulation. Pretreatment maternal effects should have been minimal in our study, as the length of our study greatly exceeded their average life span (1.5 years ± 0.05 SE) and even exceeded the longest lived individual (6 years on the predator exclosure + food grid). Our study spanned 10 generations of squirrels, and food addition resulted in a maximum sevenfold increase. Our intensive study on ground squirrels began 3 years after food addition started, and at that time densities were already about fourfold that of controls. Thus we were too late to investigate population regulatory processes, but rather could only make conclusions about limitation, and food was clearly a major limiting factor.

Although food addition had little or no effect on summer (figure 9.11, table 9.3) or winter survival (figure 9.12) or on litter sizes at emergence (figure 9.13), in arctic ground squirrels, it had marked positive effects on adult female body mass (figure 9.15), on the percentage of females weaning a litter (a 32% increase over that on controls; figure 9.13), and on earlier emergence of juveniles from the natal burrow (by 1–2 weeks; table 9.4). Similar findings have been reported for other ground squirrel species, though some have also emphasized the positive effects of food on overwinter survival. Timing of breeding, which determines the date of juvenile emergence, can affect both body size and survival of offspring as well as litter size. Parturition dates of Richardson's ground squirrels were positively related to litter size at emergence (earlier litters were larger, Dobson and Michener 1995). Rieger (1996) also found the same relationship between weaning date and litter size in Uinta ground squirrels (*S. armatus*), but also found that offspring weaned later in the season were larger than those weaned earlier. Juveniles weaned when larger in mass may have an advantage to those weaned smaller in mass; however, the greater investment by the mother may potentially affect her survival. Trombulak (1991) found in Belding's ground squirrels that food-supplemented females did not have larger litters, but weaned offspring that were 28% heavier than controls. Juveniles weaned earlier also have the potential to forage longer to accumulate the necessary fat reserves to survive hibernation. Rieger (1996) found that survival to the next spring decreased with later weaning dates in female *S. armatus*. Armitage et al. (1976) found that earlier juvenile emergence in yellow-bellied marmots (*Marmota flaviventris*) was associated with increased overwinter survival. The positive relationship between prehibernatory mass and increased overwinter survival of juvenile ground squirrels has been documented for several species of ground squirrels (*S. armatus:* Slade and Balph 1974, *S. columbianus:* Murie and Boag 1984, *S. richardsonii:* Michener 1974, Michener and Locklear 1990). However, we found no effect of food addition on survival and conclude that the major mechanism by which food addition operated in arctic ground squirrels in the boreal forest was through reproduction, not survival.

Role of Predation Predators had negative effects on aspects of the demography of both squirrel species, and reduction of predation (exclusion of large mammalian predators and reduction of avian predators under the monofilament area) ameliorated these negative effects. In red squirrels, the impact of predators was only transitory during the winter of 1991–1992 and the summer of 1992, when survival outside the predator exclosure was significantly lower than that inside it. This coincided with the highest predator–hare ratio of the decline (see chapters 13–16; Stuart-Smith and Boutin 1994). However, this increased red squirrel mortality did not translate into a marked reduction in population density, with the population easily compensating for any losses and the density remaining constant.

We were surprised that hare predators did not have a greater effect on red squirrels during the hare decline. Some reasons for the minor impact may be as follows. First, lynx were the only predators to show a major shift to squirrels, but by the time this occurred lynx numbers were already so low that they had little effect on squirrel populations. Goshawks were scarce and great horned owls tended to prey on hares throughout. Squirrels appear to be relatively safe from predation during winter. This may be due to the fact that their activity is considerably reduced during this time. With limited daylight and cold temperatures, they may only be active for a few hours. When in a nest they are simply unavailable. Extreme temperatures, such as those experienced in late January 1992, may reduce activity even further. Thus, despite constant densities, red squirrels are unreliable alternate prey because their activity patterns render them unavailable during periods when predators would need them most. It appears that predation is more important during the breeding season than it is in winter. In retrospect this is not surprising given the increased amount of time that squirrels are active and exposed to predators. It appears that food supply and predation can interact to lower survival as in summer 1992 when squirrels were without cones and predator numbers were lagging behind the hare crash.

The influence of the cyclic decline of snowshoe hares on arctic ground squirrel populations from 1990 to 1995 was clearly demonstrated by the negative population growth rates (figure 9.8) and decline in adult active season survival on all areas (including the predator exclosure) from 1991 to 1993. This is the period when predation intensity was at its highest (figure 9.9). Active season survival of adult arctic ground squirrels was lowest in 1992 and 1993, when predators were using arctic ground squirrels as alternative prey during summer (chapters 13, 15; Rohner 1994). In addition, adult survival was consistently high in 1994 and 1995, when predator biomass (and possibly predation intensity) was lowest (figure 9.9, table 9.2). Thus, predation played a major role in limiting ground squirrel populations, and much of its impact appeared to operate through changes in survival.

The ground squirrel population on the predator exclosure reached a maximum of three times the density of the control populations (figure 9.10). The predator exclosure population experienced small but nonsignificant increases in survival of adults (figure 9.11) but not of juveniles. The population within the predator exclosure and underneath the monofilament declined synchronously with that on control areas, so the monofilament was not effective at preventing the decline, and avian predators must have had access to the squirrels and compensated to some extent for the lack of large mammalian predators. On control areas in 1992 (Hubbs and Boonstra 1997), avian predators and mammalian predators caused 45% and 55%, respectively, of the identifiable kills, but on the predator exclosure (and on the predator exclosure + food) avian predators were responsible for all squirrels killed by predators.

Other studies have found increased predation on alternate prey species after declines of the principal prey. Keith and Cary (1991) observed that increased predation occurred on alternative prey (including Franklin's ground squirrels, *S. franklinii*) during a snowshoe hare decline in Alberta. Steenhof and Kochert (1988) reported that Townsend's ground squirrels (*S. townsendii*) were alternative prey for golden eagles (*Aquila chrysaetos*) during a jackrabbit (*L. californicus*) decline in Idaho. Marcstrom et al. (1989) concluded that arctic hare (*L. timidus*) densities and growth rates declined in response to increased predation by red foxes *(Vulpes vulpes)* and martens *(Martes martes)* when *Microtus* and *Clethrionomys* populations declined on two islands in the northern Baltic sea. Sutherland (1988) found that changes in survival rates of Brent geese may be due to predators such as arctic foxes *(Alopex lagopus)* switching to goose eggs and goslings as a consequence of the cyclic decline of lemmings on the Taimyr Peninsula in Siberia.

Reproduction in ground squirrels, but not in red squirrels, may also have been negatively affected by the presence of predators. More females weaned young on the predator exclosure (72%) than on the controls (45%), and litter sizes on the predator exclosure were greater than on the controls in 4 of the 5 years of the study, but juvenile emergence times were the same. We have no evidence to suggest that this was the result of food differences in the quality or quantity of food on these areas. However, the same trend in weaning rate between the predator exclosure and the controls was observed between the predator exclosure + food and the food addition site, but to a lesser degree (83% vs. 77%, respectively). In some species, the indirect effects of predators on their prey may be more important in determining changes in population growth than the direct effect of predation. Antipredatory behaviors (Holmes 1984, Carey and Moore 1986, Lima 1987) can result in less time spent foraging (Holmes 1991, Kieffer 1991) or in more time spent in protective habitats with poor-quality forage causing body condition to decline and fecundity to decrease (Hik 1995). Stress induced by the presence of predators may also have repercussions on physiological condition, causing a decline in reproductive performance (Boonstra and Singleton 1993, Hik 1995). Recent findings by Boonstra et al. (1998) indicated that snowshoe hares were chronically stressed and had low reproduction during the population decline when predation risk was high and that stress physiology and reproduction did not improve until predation risk declined. They also suggested that predator-induced stress effects may carry over into future generations, delaying population recovery after a decline. We do not know which of these processes were operating in the ground squirrels.

Interaction between Food and Predation If food and predators are influencing the dynamics of the squirrel species, was the effect additive or multiplicative? We were not able to answer this question for red squirrels, as the rabbit chow was inappropriate, we had no monofilament grid nested within this exclosure (and thus could not even partially remove the impact of avian predators), and the habitat on this treatment was more open and thus less appropriate than in prime spruce habitat. Red squirrel densities on this treatment were largely unaffected by the experimental treatment (figure 9.6). However, for ground squirrels, this treatment had the greatest, cumulative effect on densities and we conclude the effect was multiplicative. By 1995, this treatment had 60 squirrels/ha, which far exceeded density estimates on the other areas in our study (figure 9.10) and in prime natural habitat (in alpine, 5.8/ha: Green 1977, in meadows, 3–10/ha: McLean 1983). Thus, when predators are removed and food is in abundance, ground squirrel populations appear to increase without asymptoting, indicating that neither food nor predators alone can explain ground squirrel populations but that the limits of ground squirrel population densities are determined by the interaction between these two important factors.

There were three aspects of demography, which, though small, operated to increase densities in successive years. First, juvenile emergence was 1 week earlier in 2 of 5 years on the predator exclosure + food when compared with the food addition and 2 weeks earlier than that on the predator exclosure (table 9.4). Second, more adult females weaned litters on this grid (83%) than on either the food addition (77%) or predator exclosure (72%) grids (figure 9.14). Third, overwinter survival after the winter of 1993–1994 increased on food-supplemented treatments relative to unfed sites (figure 9.12). Thus, during the decline and low of the snowshoe hare cycle, ground squirrel populations are limited by an interaction between food and predation.

9.5.3 Role of Squirrels in the Boreal Forest Community

Would the dynamics of the snowshoe hare and its associated predators change if either or both of these squirrel species were absent? We cannot answer this question directly for red squirrels because the range of hares and red squirrels overlap completely. However, the arctic ground squirrel is absent over most of the boreal forest, yet the hare cycle continues, and thus ground squirrels are clearly unnecessary for its continuance. Given the constancy in numbers of red squirrels over our study, changes in squirrel densities are not necessary for the hare cycle. Nevertheless, we think that the microdynamics of the system may be affected significantly by squirrel presence. Both squirrels kill and eat baby hares (of 254 leverets radio collared during the peak of the cycle, 67% died within about 4 weeks, and of that, three-quarters were either killed or possibly killed by squirrels; O'Donoghue 1994). Thus, the presence of these squirrels provides one explanation for why conventional predators may be able to catch up to hare populations.

Squirrels may be very efficient type III predators, switching to hares at peak densities and contributing to the reduction in recruitment at the peak. This may help to explain the differences in processes that we have observed in the Yukon from what Keith (1974, 1990) observed in Alberta. Keith found that the hare decline was initiated by winter food shortage at the peak, leading to poor nutrition, some starvation losses, and a reduction in fecundity, and that the decline was maintained by predation acting in a delayed, density-dependent manner. In contrast, we have never observed absolute food shortage for hares at Kluane (chapter 6, Smith et al. 1988) and propose that predation alone is sufficient to account for the decline (Krebs et al. 1986, Trostel et al. 1987, Sinclair et al. 1988). Winter food shortage at the peak may not be seen in the Yukon where squirrels are present but may be a reality at Keith's study site where the impact of squirrels is less (arctic ground squirrels are not present, and the habitat is less suitable for red squirrels). Thus squirrels may shift the mechanisms acting during the hare decline from a starvation–predation scenario to a pure predation scenario.

Red squirrels and northern red-backed voles may be possible competitors for access to spruce seed. Given the large numbers of cones harvested by the red squirrels (up to 16,000 per territory in nearby Alaska; M. C. Smith 1968), the seeds from these cones are thus not available for the voles. However, we review evidence in chapter 10 that spruce seed is a poor food for these voles and present evidence that vole population dynamics appear to operate largely independent of the spruce seed crop. Given that the dynamics of red-backed vole populations in deciduous forests elsewhere are tightly linked to that of tree seed production (Jensen 1982, Pucek et al. 1993, Wolff 1996), what is the explanation for our results? One possibility is that red squirrels are such efficient harvesters of cones in boreal forests that spruce seeds do not become available for secondary consumers such as voles often enough and that mast years are too rare to specialize on.

9.6 Conclusions

Red squirrel populations showed little variation over the hare cycle. Larger cone crops in one year were positively related to squirrel density in the next year. Adult survival was not related to cone supply, whereas reproduction was, with more young being produced in the last half of the study when cone crops were above average.

The experimental treatments were largely ineffective in influencing red squirrel population dynamics: the food addition had no effect on populations; the exclusion of predators had an effect, but only during one summer when hare predators were high and spruce cone crops were low. The interaction treatment (food addition and exclusion of predators) had no effect, and the fertilization may have had a small negative effect, but the reason is not clear.

Populations of arctic ground squirrels declined and increased in tandem with the decline and increase of snowshoe hares from 1990 to 1996. Increased predation and weather contributed to lower survival and reproduction, causing a decline of control populations from 1991 to 1993. Populations did not show positive growth until predators were at their lowest densities from 1994 to 1996.

Exclusion of predators caused a twofold increase in ground squirrel densities, addition of food a fivefold increase, and both exclusion of predators and food addition an 11-fold increase. Predators were largely responsible for the decline of ground squirrel populations, independent of treatment. Absence of predators improved weaning rate. The benefits of food acted primarily by improving aspects of ground squirrel reproduction (improved weaning success, earlier emergence of young from the natal burrow, and higher adult female body weight). We conclude that ground squirrel populations are predominately limited by the multiplicative interaction between food and predation through changes in reproduction of adult females. Fertilization had strong negative effects on arctic ground squirrel populations, and we suggest that ground squirrels would not be present in the boreal forest if it were not nutrient limited.

Red squirrel and arctic ground squirrel predation on hare leverets during the peak of the hare cycle may be key contributors to slowing down hare population growth sufficiently to allow predators time to catch up. They thus prevent hares from overgrazing their food supply.

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