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RED SQUIRREL POPULATION DYNAMICS. I. THE EFFECT OF SUPPLEMENTAL FOOD ON DEMOGRAPHY

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SUMMARY

(1) We examined the effect of food availability on the population dynamics of red squirrels. A temporary, *ad libitum* food addition was conducted during two summers in Douglas fir (low population density) and white spruce (high population density) forest habitats from 1985 to 1988 in south-central British Columbia, Canada.

(2) The addition of supplemental food resulted in a strong increase in recruitment, primarily by juvenile immigrants in autumn. Increased recruitment caused a fourfold increase in population density in fir habitat and a twofold increase in spruce habitat. Both recruitment to the food-supplemented grids and the decline in density following the removal of food were density-dependent.

(3) Supplemental food had no clear effect on juvenile or adult weights, juvenile growth rates, juvenile or adult survival, reproductive parameters or sex ratios.

(4) The difference in red squirrel population density in the two habitats was due to higher average food availability in white spruce habitat. The availability of excess food during the food addition period indicated that factors other than food availability limited the population at high density.

INTRODUCTION

Two critical questions concerning animal abundance are (i) what causes differences in population density between habitats, and (ii) what influences density within a specific habitat (Chitty 1960). Food availability has long been recognized as one of the major factors influencing the population dynamics of animals (Lack 1966; Newton 1980; Dobson & Kjelgaard 1985; Martin 1987; Arcese & Smith 1988; Boutin 1990). Although the effect of food on population size and reproduction has been well established, other factors including harsh weather, disease, predation or spacing behaviour can limit population density below the level set by food. In an attempt to clarify the role of food and its effect on animal populations, a growing number of studies have experimentally manipulated food availability and monitored population responses (see Boutin 1990 for a review).

The red squirrel (*Tamiasciurus hudsonicus* Erxleben) is a small, arboreal sciurid commonly found in the boreal forests of North America. Studies by C. Smith (1968), M. Smith (1968), Erlien & Tester (1984) and Halvorson (1984) have suggested that the population density of this species fluctuates and may be closely related to the abundance of cone crops (mast). However, Rusch & Reeder (1978) reported that red squirrel populations remained stable despite fluctuations in food availability.

They suggested that spacing behaviour regulates density about a level set during years of food scarcity. In an initial test of the above hypothesis, Sullivan & Sullivan (1982) noted a positive response to the addition of supplemental food in the closely related Douglas squirrel (*T. douglasii*). However, the use of trapping lines made estimates of changes in density tenuous. In a subsequent investigation, Sullivan (1990) found that the population density of red squirrels did increase during a long-term feeding study.

It is not clear whether red squirrel populations track short-term changes in food availability or if an inflexible territory size leads to population stability despite large changes in food availability. In this manuscript, we describe the effect of adding a short-term provision of supplemental food on the demography of a population of red squirrels in poor (low population density, Douglas fir) and good (high population density, white spruce) forest habitats. We used supplemental food to determine whether food availability caused the difference in density between the two habitats and if food is the main factor affecting density within a habitat. If red squirrel densities are limited solely by food availability, we predicted that population density should rise to that level. If food limits population size, we also predicted that body weight, growth rate, survival and reproduction would increase.

We used a temporary food addition to simulate periodic fluctuations in natural cone mast, the primary overwinter food of the red squirrel (C. Smith 1968; M. Smith 1968). In addition to providing what we believe is a more realistic simulation of natural food conditions than a long-term food addition, a brief food addition is not as likely to attract predators to the food addition area after local population density increases (the 'pantry effect', Batzli 1983). By removing supplemental food at the end of the pulse, we were also able to monitor the response of a high density population exposed to control food conditions.

METHODS

Study area

The study area was located in south-central British Columbia, Canada, near the village of 100 Mile House (51°42′N; 101°24°W). This region is within the Douglas fir-pinegrass (northern phase) subzone of the Interior Douglas Fir biogeoclimatic zone. Topography in the area is rolling to hilly with a mean elevation of 950 m (Krajina 1969; Annas & Coupe 1979). The climate is characterized by warm, dry summers and cold, dry winters with mean July and January temperatures of +16 and −10 °C respectively and a mean annual precipitation of 40 cm. Predominant coniferous overstorey species in the area are lodgepole pine (*Pinus contorta* Dougl.) and Douglas fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco). White spruce (*Picea glauca* (Moench) Voss) is common in mesic sites along watercourses and in poorly drained areas. Deciduous overstorey species include aspen (*Populus tremuloides* Michx.) and black cottonwood (*P. trichocarpa* Torr. & Gray). A more detailed description of the vegetation in this region is presented by Annas & Coupe (1979).

Experimental design

Eight study plots were established in Douglas fir and white spruce habitat between

1985 and 1987. In fir habitat, a replicated design (two control, two food addition) was used in 1986 and 1987. In spruce habitat, there was one control and one food addition in 1986 and two of each in 1987. Each study plot was initially surveyed as a square 10 × 10 grid with 30-m intervals between stations on each row (9 ha), but modifications were required because of patchy habitat on some grids. One spruce control and one spruce food addition grid were rectangular (8 × 12, 7 × 14, respectively) and two spruce grids were only 7·1 and 7·8 ha due to large areas of unsuitable habitat (sedge meadows, *Carex* sp.) within the plots.

Red squirrel populations

Squirrels were captured in live-traps (Model 201, Tomahawk Live Trap Co., Tomahawk, Wisconsin) baited with sunflower seed (10 g) and a slice of apple. We placed traps at every second station on the grid, resulting in approximately five traps ha^{-1}. Squirrel populations were censused by live-trapping every 3–5 weeks during April–December and every 6–8 weeks during January–March from June 1985 to June 1988. From June to December 1988, populations were censused every 6–9 weeks. In total, there were thirty-six trapping sessions between June 1985 and December 1988. Inclement weather during winter (November–March) necessitated irregular trapping during this period.

During trapping sessions, traps were set for 2 days and were checked three times. Traps were opened shortly after dawn on the first day, checked 4 h later and again in the evening before being closed for the night. On the second day, traps were set and checked only once in the morning. When supplemental food was available on the treatment grids, feeders were closed during the trapping session. All animals were identified with numbered metal ear tags and some animals were fitted with coloured vinyl ear tags for individual identification at subsequent captures. When squirrels were captured, we recorded the ear-tag number, location, weight (to ± 5 g on a Pesola spring-balance), sex and breeding condition. We used weight and pelage characteristics to classify animals as either juveniles (< 170 g) or adults when they were first captured. In autumn, the juvenile pelage is softer, longer and often more grey-brown in colour than that of adults (Layne 1954). The breeding condition of males was evaluated by palpating the testes when it was not obvious whether the animal was scrotal or abdominal. Females were considered to be in breeding condition if they were obviously pregnant (high body weight and a distended lower abdomen), lactating (verified through palpation) or had developed nipples and mammae showing signs of nursing (matted fur or small wounds).

Demographic parameters

To assess the effects of changing food availability on population demography, we monitored trappability, population density (the number of squirrels captured on the study areas), body weight and growth rate, recruitment, survival, reproduction and sex ratios. Trappability was calculated as (number trapped/Jolly population estimate (Seber 1982)). Population density was estimated using both the minimum number alive (MNA) (Krebs 1966) and Jolly–Seber (JS) estimates (Seber 1982). During the time when supplemental food was present, the JS estimate was 1·3 times higher than the MNA estimate on the food addition areas and 1·2 times higher on the control areas. As the JS and MNA estimates indicated a similar pattern of population change, we used the JS estimate to compare differences in trappability, population size and survival. We used the more conservative MNA estimate (Jolly & Dickson 1983; Krebs & Boonstra 1984) to examine recruitment in relation to population density.

We defined recruits as those animals which were able to establish themselves as residents. All animals captured for the first time were classified as newcomers. Many of these animals were immigrants but some are known to have been born on the study grids as they were captured in their nest or at the base of the nest tree while still very small. Squirrels which were captured during a minimum of two consecutive trapping sessions (i.e. they were present in the area for a minimum of 4 weeks) were considered residents and classified as recruits. This appeared to be a good criterion for assessing recruitment since many of these squirrels were observed defending territories (W. Klenner, unpubl.). To compare recruitment between treatments, we averaged the 1986 and 1987 live-trapping data. We divided the period from June to February into three, 3-month periods corresponding to before, during and after supplemental food and compared recruitment within each of these periods.

Mean monthly survival was calculated as the geometric mean of Jolly's estimates of survival between trapping sessions. Reproduction was evaluated by estimating the proportion of animals which were in breeding condition and the length of the breeding season which was calculated as the number of weeks during which a female was either pregnant or lactating.

Supplemental food and cone mast

Supplemental food (sunflower seed, *Helianthus annuus* L.) was added from 10 August to 23 October in spruce habitat and from 19 August to 20 November in Douglas fir habitat in 1986. In 1987, food was added in spruce habitat from 18 July to 8 October and from 29 July to 20 November in Douglas fir habitat. When supplemental feeding was terminated, the remaining seed was removed from feeders. The timing and distribution of food was designed to simulate a large cone crop which would remain available to squirrels for approximately 3 months. Sunflower seed was distributed in 5-l plastic pails which were attached to large trees and sheltered from rain with a cover (30 × 30 cm). Feeders were located approximately 2 m above ground in a 12 × 12 square grid at 30-m intervals along rows. Each food addition plot had 100 feeders on the central 9-ha plot and an additional forty-four feeders in a surrounding buffer strip. Each grid received approximately 160 kg of seed per month. Seed was provided *ad libitum* and was replenished before feeders were empty.

Natural cone mast was assessed using procedures outlined in the British Columbia Ministry of Forests cone collections guidelines (Eremko, Edwards & Wallinger 1989). Cone mast was ranked on a scale of one (very light) to seven (very heavy) by subjectively evaluating 200 trees on each of the study plots. Trees were chosen for evaluation without looking at their crowns to prevent bias. As a general guideline, trees assigned a very heavy rating had a minimum of 2000 cones.

Statistical analyses

To analyse data which were not independent (the same animals were often captured during consecutive trapping sessions), we used a repeated-measures ANOVA to examine changes over time (Zar 1984). To examine only the specific time when supplemental food was present or after it had been removed, we averaged the JS density estimates from three trapping periods before food was added, when it was present and during the 6–8-month period after the end of the food addition. We used a *t*-test to examine these localized differences in density between control and treatment grids.

To evaluate differences between treatments within a period, we used a two-factor ANOVA to examine habitat (fir vs. spruce) and treatment (control vs. food addition) effects as well as the interaction between factors. When the interaction term was significant, we used multiple contrasts (Scheffés test, Zar 1984) to examine differences between means.

Unless otherwise indicated, mean values and comparisons are based on two replicates for each treatment. Each replicate represents the mean value for the animals monitored on each study plot. Where treatments on a plot were repeated in 1986 and 1987, the data from each year were used to calculate a mean value that was used to represent one replicate. Data were log-transformed or, where proportions were being compared, arcsine square root transformed before analyses were carried out using the SYSTAT statistical analysis package (Wilkinson 1988). The level of significance was set at $\alpha = 0{\cdot}05$.

RESULTS

Direct observations indicated that red squirrels readily used the supplemental food and also cached it in their middens as they would cone mast. Sunflower seeds appeared to be a desirable food. When squirrels emerged from their nests at dawn, they would often feed on sunflower seeds at a feeder for 5–10 min before foraging elsewhere. Also, during and after a trapping session, resident squirrels would search the trap locations and feed on spilled seeds. In addition to using the sunflower seed, squirrels continued to eat naturally available foods such as cones and fungi.

Trappability

We calculated the overall trappability of juveniles and adults as well as trappability during the period when supplemental food was available (Table 1). The overall trappability of juveniles was greater in spruce than in fir habitat but was not affected by the food treatment (ANOVA, habitat; $F = 62{\cdot}071$, d.f. = 1,4, $P < 0{\cdot}001$: food treatmènt; $F = 1{\cdot}33$ d.f. = 1,4, $P = 0{\cdot}313$). Similarly, juvenile trappability during the periods when supplemental food was present was greater in spruce than in fir habitat (ANOVA, habitat; $F = 16{\cdot}152$, d.f. = 1,4, $P = 0{\cdot}016$: food treatment; $F = 0{\cdot}001$, d.f. = 1,4, $P = 0{\cdot}981$).

There were no significant differences in the trappability of adults in relation to either habitat or food treatment during the entire study period (ANOVA, habitat; $F = 5{\cdot}047$, d.f. = 1,4, $P = 0{\cdot}088$: food treatment; $F = 3{\cdot}342$, d.f. = 1,4, $P = 0{\cdot}142$) or while supplemental food was present (habitat; $F = 2{\cdot}792$, d.f. = 1,4, $P = 0{\cdot}170$: food treatment; $F = 0{\cdot}854$, d.f. = 1,4, $P = 0{\cdot}408$).

Population density

The addition of supplemental food increased population density in both fir and spruce habitats (Fig. 1). The change in density in fir habitat was greater than in spruce

TABLE 1. Estimates of Jolly trappability (mean ± 1 S.E.) for juvenile and adult red squirrels. Values are mean percentage trappability (number caught/Jolly–Seber population estimate × 100) and are based on the mean of two replicates for each treatment

	Juveniles		Adults	
Treatment	Total*	Food†	Total	Food
Fir control	90·9 (0·8)	83·1 (4·2)	70·3 (9·6)	66·6 (20·9)
Fir treatment	92·3 (0·6)	87·3 (0·8)	62·4 (3·1)	53·9 (5·9)
Spruce control	99·2 (0·8)	97·8 (2·2)	83·9 (1·7)	82·4 (3·2)
Spruce treatment	96·1 (1·0)	93·5 (2·0)	72·5 (2·6)	75·7 (6·5)

* Represents trappability during entire period of study.

† Represents trappability during the two periods (1986 and 1987) when supplemental food was available on the treatment grids.

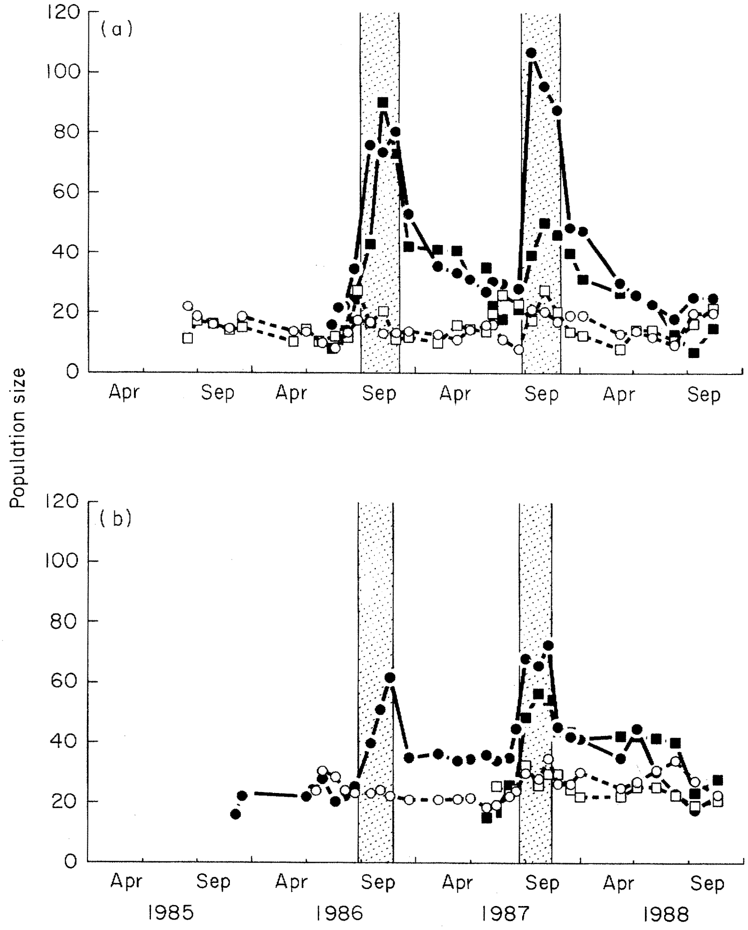

FIG. 1. Jolly–Seber estimate of red squirrel population size on each 9 ha study plot in (a) Douglas fir habitat and, (b) white spruce habitat from 1985 to 1988. (○) and (□) represent controls, (●) and (■) represent food addition treatments. Shaded area indicates the period during which supplemental food was available.

habitat (4·1-fold vs. 2·1-fold), but populations in both habitats reached approximately the same density. Although supplemental food was available for a longer period (approximately 25%) in fir than in spruce habitat, this difference did not increase the response to supplemental food. In fir habitat, population size increased rapidly after supplemental food was provided and reached an asymptote within 6 weeks. Despite the continued availability of supplemental food for an additional 2 months, population size did not increase further. A repeated-measures ANOVA indicated that in fir habitat, the overall food effect was significant ($F = 23{\cdot}844$, d.f. = 1,2, $P = 0{\cdot}039$) while the time ([trapping session] $F = 17{\cdot}582$, d.f. = 24,48 $P < 0{\cdot}001$) and food × time interaction effects ($F = 4{\cdot}823$, d.f. = 24,48, $P < 0{\cdot}001$) were both highly significant. In spruce habitat, the results were similar (food effect; $F = 29{\cdot}679$, d.f. = 1,2, $P = 0{\cdot}032$: time effect; $F = 4{\cdot}673$, d.f. = 12,24, $P = 0{\cdot}001$) except that the food by time interaction was not significant ($F = 1{\cdot}611$, d.f. = 12,24, $P = 0{\cdot}154$).

We examined squirrel population density on the control and food treatments before and during the time when supplemental food was present by comparing the average JS density (averaged across three trapping periods). In fir habitat, control and treatment grids were not significantly different before supplemental food was added in 1986 or 1987 (1 May–18 July; $t = 1{\cdot}31$, d.f. = 2, $P = 0{\cdot}321$; $t = 2{\cdot}76$, d.f. = 2, $P = 0{\cdot}11$, respectively). While supplemental food was present (1 August–early November), differences between the control and food grids were significant in 1986 but not in 1987 ($t = 17{\cdot}76$, d.f. = 2, $P = 0{\cdot}003$; $t = 3{\cdot}01$, d.f. = 2, $P = 0{\cdot}095$, respectively). In spruce habitat, squirrel populations on control and treatment grids were not different before supplemental food was added (1 May–20 July, 1987; $t = 0{\cdot}35$, d.f. = 2, $P = 0{\cdot}759$) but were significantly different while supplemental food was present (21 July–20 October, 1987; $t = 3{\cdot}92$, d.f. = 2, $P = 0{\cdot}034$). In 1986, squirrel populations on the control and treatment grids showed the same trend as in 1987 (Fig. 1).

Body weight and growth rate

There were no consistent differences in mean adult body weight between the control and food treatments in either fir or spruce habitat. When averaged across the 3 years of live-trapping, the weights of both adult males and females in fir control and treatment habitat were very similar (males: 219·8 vs. 219·9 g; females: 217·2 vs. 215·2 g, respectively). In spruce habitat, we noted the same pattern between control and treatment areas (males: 220·8 vs. 224·6 g; females: 211·1 vs. 212·8 g, respectively). A two-factor repeated-measures ANOVA over seventeen trapping sessions indicated that there were no significant differences in adult body weight between habitats or food treatments (males; habitat, $F = 1{\cdot}685$, d.f. = 1,4, $P = 0{\cdot}264$; food treatment, $F = 0{\cdot}818$, d.f. = 1,4, $P = 0{\cdot}417$: females; habitat, $F = 1{\cdot}579$, d.f. = 1,4, $P = 0{\cdot}277$; food treatment, $F = 0{\cdot}001$, d.f. = 1,4, $P = 0{\cdot}985$). Adult males and females weighed approximately the same in fir habitat but in spruce, males tended to be approximately 10 g heavier than females (222·7 vs. 212·0 g).

To determine if changes in the body weights of certain individuals were being masked by calculating mean body weights, we examined sixteen randomly selected individuals (eight control, eight treatment). Again, there were no clear differences in adult body weight or rate of weight loss overwinter by adults between control and food-supplemented animals.

We examined the growth rates of juveniles in fir and spruce habitat by plotting the change in mean body weight over time. In 1986, juvenile males from the food addition areas in fir habitat reached a higher body weight by the end of summer than males on the control grids (207 g vs. 195 g). However, this pattern was not repeated in 1987. There was no consistent difference between juvenile female growth rates on control and food-supplemented areas. In spruce habitat, juvenile male growth rates between treatments were similar in 1986 and 1987 but juvenile females from the food addition areas appeared to reach a higher body weight in the winter of 1987 (208 g vs. 194 g). Because of the low number of recruits in control habitat (one to three animals), these results could not be tested statistically and must be interpreted with caution.

Recruitment and population decline

The addition of supplemental food had a strong positive effect on recruitment in both fir and spruce habitat. We were not able to establish the origin of most recruits, but because there were few breeding females and many newcomers, most of these animals were immigrants. The number of newcomers (Fig. 2) increased to an average of twenty-five during the second trapping period when supplemental food was available. In both fir and spruce control habitat, an average of eight newcomers were captured during this period.

The number of recruits also increased (Fig. 3). The apparent lag in recruitment which continued after the food addition ended is an artefact of how we defined recruits. Individuals had to be resident for two consecutive trapping sessions before being considered recruits after the second capture. To compare recruitment on control and food addition grids, we examined the cumulative totals (averaged across 1986 and 1987) of newcomers and recruits during three trapping periods before, while supplemental food was present, and after feeding ended. For this analysis, we assigned individuals which became recruits to the trapping period when they were first captured. The number of newcomers and recurits did not differ between habitats or food treatments before food was added (ANOVA, newcomers; habitat, $F = 0{\cdot}023$, d.f. = 1,4, $P = 0{\cdot}887$; food treatment, $F = 2{\cdot}443$, d.f. = 1,4, $P = 0{\cdot}193$: recruits; habitat, $F = 0{\cdot}000$, d.f. = 1,4, $P = 1{\cdot}000$; food treatment, $F = 0{\cdot}000$, d.f. = 1,4, $P = 1{\cdot}000$). While supplemental food was present, the number of newcomers and recruits greatly increased on the food addition areas (newcomers; habitat, $F = 2{\cdot}056$, d.f. = 1,4, $P = 0{\cdot}225$; food treatment, $F = 275{\cdot}433$, d.f. = 1,4, $P < 0{\cdot}001$: recruits; habitat, $F = 0{\cdot}404$, d.f. = 1,4, $P = 0{\cdot}560$; food treatment, $F = 168{\cdot}915$, d.f. = 1,4, $P < 0{\cdot}001$). Although males and females were equally successful at becoming recruits, a higher proportion of both sexes did so in areas with supplemental food (50%) than in control habitat (25%). After food was removed, the number of newcomers was similar between habitats and food treatments (ANOVA, habitat, $F = 4{\cdot}169$, d.f. = 1,4, $P = 0{\cdot}111$; food treatment, $F = 0{\cdot}092$, d.f. = 1,4, $P = 0{\cdot}777$) but there were more recruits in fir than in spruce habitat (habitat, $F = 19{\cdot}926$, d.f. = 1,4, $P = 0{\cdot}011$; food treatment, $F = 2{\cdot}844$, d.f. = 1,4, $P = 0{\cdot}167$).

We examined the recruitment rate and the proportion of newcomers which became residents as density increased during the time when supplemental food was available. For this analysis, we considered recruitment only on the food treatment grids to avoid confounding food availability and density effects. In both fir and

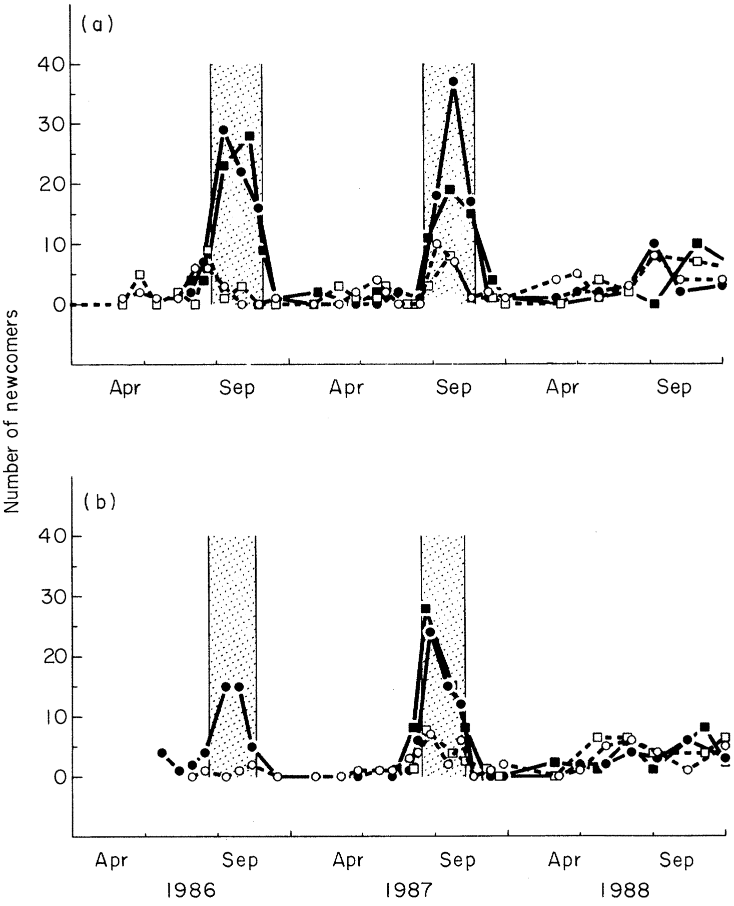

FIG. 2. The number of newcomers (juvenile squirrels captured for the first time) in (a) Douglas fir and (b) white spruce habitat. (○) and (□) represent controls, (●) and (■) represent food addition treatments. Shaded area indicates the period during which supplemental food was available.

spruce habitat, the recruitment rate was density-dependent (Fig. 4a, c); as density on the study plots increased, the recruitment rate decreased. At the same time, the proportion of newcomers which became recruits also decreased (Fig. 4b, d).

Newcomers were present in both fir and spruce habitat during the three trapping sessions when supplemental food was available (Fig. 2). Although the number of newcomers captured in spruce habitat decreased towards the end of the food addition, there was still an average of ten newcomers captured during the last trapping session while food was present in 1987. We did not observe any physical or behavioural differences between newcomers captured early in the season, towards the end of the supplemental food period, or animals which became recruits. Pelage condition and the incidence of wounds appeared to be similar between these types of animals. There were no significant differences in body weight between recruits and newcomers in relation to the food treatment (ANOVA, $F = 0{\cdot}177$, d.f. $= 1,4$, $P = 0{\cdot}696$) but there

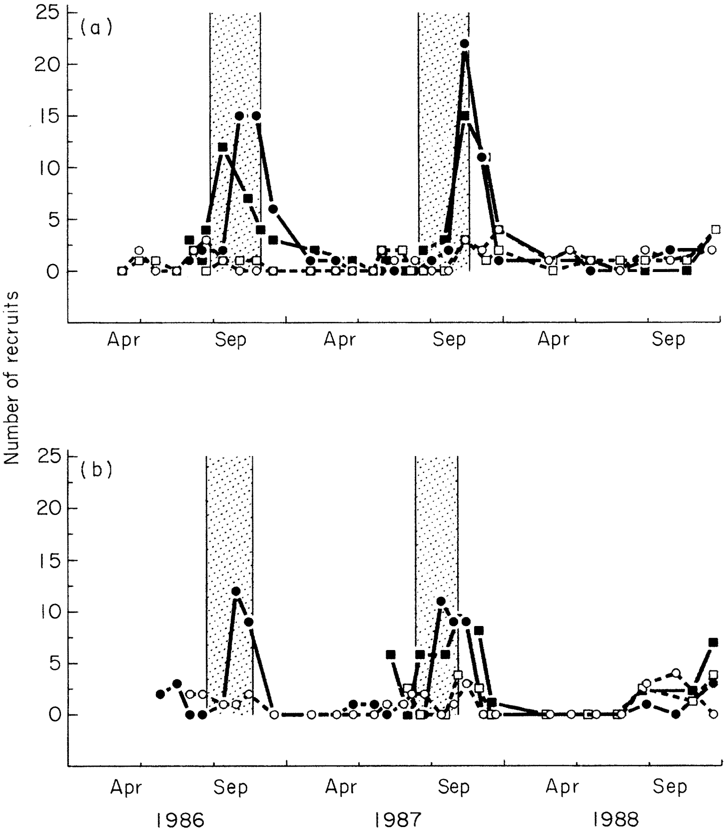

FIG. 3. The number of recruits (juvenile squirrels captured in two consecutive trapping periods) in (a) Douglas fir and, (b) white spruce habitat. (○) and (□) represent controls, (●) and (■) represent food addition treatments. Shaded area indicates the period during which supplemental food was available.

were significant differences between habitats ($F = 14{\cdot}690$, d.f. = 1,4, $P = 0{\cdot}019$). In mid-October, newcomers in fir habitat were on average 5·1 g heavier than recruits while in spruce habitat, they averaged 15.9 g less.

During the 7-month period after supplemental feeding ended each year, the rate of population decline was not different between habitats but was greater on areas which had received supplemental food (Table 2; ANOVA, habitat, $F = 3{\cdot}720$, d.f. = 1,4, $P = 0{\cdot}126$; food treatment, $F = 22{\cdot}366$, d.f. = 1,4, $P = 0{\cdot}009$). Population size in fir treatment habitat decreased at seven times the rate in fir control habitat and over twice the rate in either spruce habitat (multiple contrasts, $F = 26{\cdot}284$, d.f. = 1,4, $P < 0{\cdot}007$). The rate of population decline in fir control, spruce control and spruce treatment habitat was not significantly different (multiple contrasts, $F = 3{\cdot}921$, d.f. = 1,4, $P = 0{\cdot}119$). Although the average rate of population decrease was greatest in the fir treatment areas, the monthly decline did not follow a clear density-dependent pattern (Fig. 5).

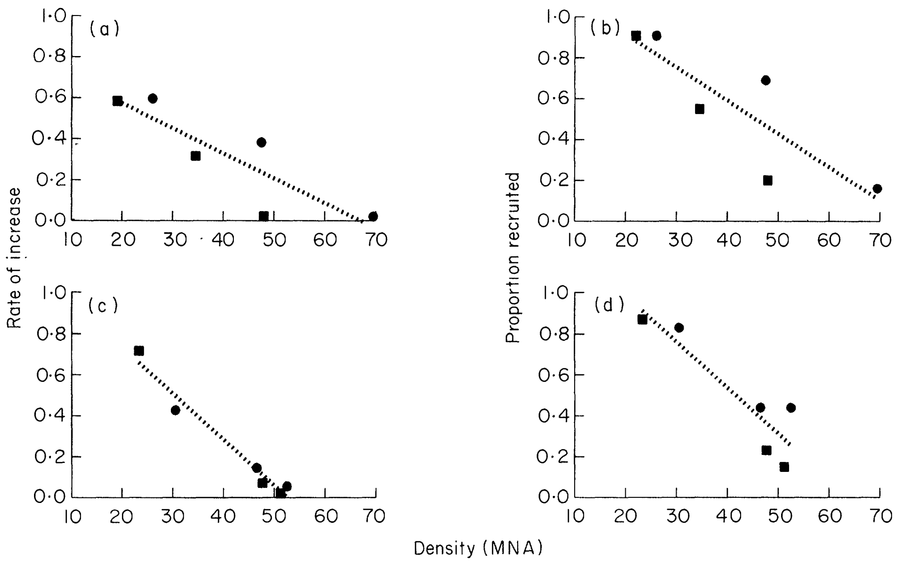

FIG. 4. The instantaneous monthly rate of population change (a, c) and the proportion of newcomers which became recruits (b, d) in Douglas fir (a, b) and white spruce habitat (c, d). Data represent the mean values for each replicate (averaged over 1986 and 1987) during three trapping sessions when supplemental food was available: (●) replicate 1, (■) replicate 2. Dotted lines indicate trends as estimated by least squares regression.

TABLE 2. Mean monthly instantaneous rate of population change (± 1 S.E.) on control and food treatment areas during the 7-month period after supplemental feeding was discontinued

Treatment	Rate of change*	
Fir control	−0·035	($1{\cdot}50 \times 10^{-4}$)
Fir treatment	−0·250	(0·017)
Spruce control	−0·052	(0·002)
Spruce treatment	−0·118	(0·057)

* Values represent an average of the 1986 and 1987 estimates for each of the two replicates and are based on the Jolly–Seber estimate of population density.

Survival

We calculated Jolly survival of juveniles during the time when supplemental food was available and during the 5-month period after feeding was discontinued (Table 3). While supplemental food was available, survival in fir and spruce habitat was similar (ANOVA, $F = 0{\cdot}168$, d.f. = 1,4, $P = 0{\cdot}703$) but there was a significant difference in relation to the food treatment and a significant food × habitat interaction (food treatment; $F = 30{\cdot}090$, d.f. = 1,4, $P = 0{\cdot}005$: food × habitat interaction; $F = 37{\cdot}704$, d.f. = 1,4, $P = 0{\cdot}004$). Juvenile survival on the fir control areas was lower

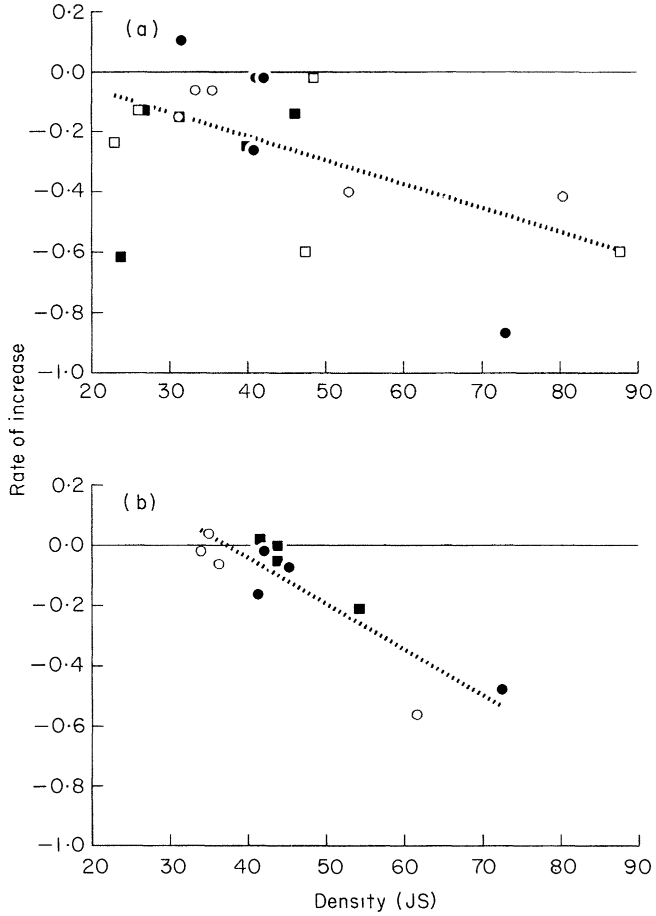

FIG. 5. The instantaneous monthly rate of population change in (a) Douglas fir and, (b) white spruce habitat. (○) and (□) represent 1986 treatment grids, (●) and (■) 1987 treatment grids. The data represent five trapping sessions over a 7-month period after supplemental feeding was discontinued. Dotted lines indicate trends as estimated by least squares regression.

TABLE 3. Mean monthly Jolly survival (± 1 S.E.) of juvenile red squirrels. Values represent the average of 1986 and 1987 estimates for each of the two replicates

Treatment	Food*		Post-food†	
Fir control	0·52	(0·02)	0·92	(0·03)
Fir treatment	0·81	(0·04)	0·75	(0·03)
Spruce control	0·68	(0·01)	0·90	(0·03)
Spruce treatment	0·67	(0·03)	0·83	(0·06)

* Juvenile survival during the 3-month period when supplemental food was available.

† Juvenile survival during the 5-month period after supplemental feeding was discontinued.

than on the other treatments (multiple contrasts, $F = 17{\cdot}374$, d.f. = 1,4, $P = 0{\cdot}014$). After supplemental feeding was discontinued, survival was similar between habitats but was lower on the areas which had received supplemental food (ANOVA, habitat, $F = 0{\cdot}716$, d.f. = 1,4, $P = 0{\cdot}445$; food treatment, $F = 9{\cdot}262$, d.f. = 1,4, $P = 0{\cdot}038$).

Adult survival ranged from 86 to 95% between treatments before, during and after the addition of supplemental food. There were no significant differences in average adult survival in relation to habitat or food treatment either before (ANOVA, habitat, $F = 2{\cdot}850$, d.f. = 1,4, $P = 0{\cdot}167$: food treatment, $F = 0{\cdot}083$, d.f. = 1,4, $P = 0{\cdot}787$), during (habitat, $F = 3{\cdot}229$, d.f. = 1,4, $P = 0{\cdot}147$: food treatment, $F = 4{\cdot}678$, d.f. = 1,4, $P = 0{\cdot}097$), or after (habitat, $F = 2{\cdot}729$, d.f. = 1,4, $P = 0{\cdot}174$: food treatment, $F = 0{\cdot}891$, d.f. = 1,4, $P = 0{\cdot}399$) the addition of supplemental food.

The decline in density on the food-supplemented areas in late winter may be the result of *in situ* mortality (e.g. starvation or predation) or emigration. Most of the decrease in density occurred in late winter and was attributable to the loss of juveniles which had immigrated during the time when supplemental food was available. Although we have few direct observations on the fate of the animals which disappeared after supplemental feeding ended, there were indications that squirrels were emigrating rather than dying on the grids. In March, we began to capture animals from the treatment grids on the adjacent (approximately 1 km away) control areas. In the spring of 1987 and 1988, we caught nineteen suqirrels which had moved from the treatment to the control grids. Of these, five eventually became permanent residents (four of fifteen in fir habitat; one of four in spruce habitat), suggesting that a large proportion of the population decline on the treatment areas was due to emigration.

Breeding

There was little difference in the proportion of either adult or juvenile males in breeding condition, or in the length of the breeding season. All males became scrotal in late winter or early spring. Adult females on one of the food treatment areas reached breeding condition 1 month earlier in 1988 but this difference was not significant (ANOVA, habitat, $F = 3{\cdot}251$, d.f. = 1,4, $P = 0{\cdot}143$; food treatment, $F = 1{\cdot}193$, d.f. = 1,4, $P = 0{\cdot}226$). Yearling females on the food addition areas came into breeding condition about 1 month earlier than on the control areas in both 1987 and 1988 but the low number of females on the control areas (from zero to two) precludes statistical comparisons.

Habitat type or the addition of supplemental food did not have a significant effect on the length of the breeding season as estimated by the number of weeks females were pregnant or lactating (ANOVA, habitat, $F = 1{\cdot}778$, d.f. = 1,4, $P = 0{\cdot}253$; food treatment, $F = 0{\cdot}010$, d.f. = 1,4, $P = 0{\cdot}926$). From 1986 to 1988, the breeding season ranged from 4·0 to 10·0 weeks $\bar{x} = 5{\cdot}5$) across all treatments. We did not observe any individuals which were pregnant or lactating for more than 10 weeks, indicating that females did not have more than one litter per year.

Sex ratios

The sex ratio of adults (proportion of males) was similar between habitats (fir = 0·51, spruce = 0·53; ANOVA $F = 0{\cdot}121$, d.f. = 1,4, $P = 0{\cdot}746$) and food treatments (control = 0·54, food = 0·50; $F = 0{\cdot}245$, d.f. = 1,4, $P = 0{\cdot}647$). Similarly, there was no difference in the sex ratio of juvenile recruits between fir and spruce habitat (fir = 0·50, spruce = 0·33; ANOVA, $F = 3{\cdot}917$, d.f. = 1,4, $P = 0{\cdot}119$) but there were more male recruits on the food supplemented areas (control = 0·26, food = 0·55; $F = 8{\cdot}357$, d.f. = 1,4, $P = 0{\cdot}045$).

DISCUSSION

In response to supplemental food, the population density of red squirrels in both fir and spruce habitat increased to approximately the same level. The initial density in Douglas fir habitat was lower, and hence the fourfold increase there was greater than the twofold increase in white spruce habitat. These results indicate that red squirrel populations in both habitats are limited by food, but that food is more strongly limiting in Douglas fir habitat. Although population density increased when supplemental food was added (and continued to stay high until the end of the food addition), excess food remained and other factors prevented a further increase.

The increase in the population density of red squirrels after supplemental food was added agrees with the results reported by Sullivan & Sullivan (1982) and Sullivan (1990). Studies on other sciurids have also noted a strong increase in density after the addition of supplemental food. Dobson & Kjelgaard (1985) observed an 85% increase in the population size of Columbian ground squirrels supplied with additional food. Mares *et al.* (1982) and Sullivan, Sullivan & Krebs (1983) also reported an increase in population density after supplying supplemental food to two species of chipmunks (*Tamias* spp.).

In contrast, Havera & Nixon (1980) found that supplemental feeding had little effect on grey and fox squirrel populations. During their study, natural mast crops were above average and they indicate that the supplemental food used (corn) may not have been nutritionally adequate. Similarly, Wolff (1985) reported that supplemental food had little effect on the population density of two species of deermice (*Peromyscus* spp.), but he provided no evidence that the laboratory mouse chow provided was utilized. Other food addition studies on deermice (see Taitt 1981) have demonstrated a strong positive effect on density. In a review of food addition studies, Boutin (1990) concluded that most studies have shown an effect on density, but that an increase in density is less likely to occur when natural food levels are high.

In 1987, the increase in red squirrel density in fir habitat during the supplemental food period was not significant because of high variability between replicates. On one of these areas, black bears (*Ursus americanus* Pallas) interfered with the experiment for the first 6 weeks of the food addition by tearing feeder pails from trees. Although the bears consumed some of the sunflower seed, we believe that the lesser response that we observed was the result of seed being scattered on the ground. Fewer newcomers were captured in this area, possibly because there was little incentive for squirrels to enter traps when there were large amounts of seed on the ground. However, both replicate areas showed a greater increase in density than on either of the controls.

During 1986 and 1987, cone crops were light to moderate in both fir and spruce habitat (Table 4). The only large cone crop we observed was in white spruce habitat in 1985. We observed large cone crops on individual trees or small groups of trees (less than five) in both fir and spruce habitat but this was not as extensive as in 1985. As our food addition experiments followed the large spruce cone crop in 1985, our

Table 4. Estimates of cone crop abundance in Douglas fir and white spruce habitat

Year	Douglas fir*	White spruce
1985	Very light	Very heavy
1986	Light	Light
1987	Light–moderate	Light
1988	Light	Light

* Estimates based on subjective evaluations using proceedures outlined in Eremko, Edwards & Wallinger (1989). See text for details of the methods used.

results provide little insight into whether red squirrels are food limited when cone mast is abundant. However, we would predict that squirrels are not limited by food availability during these years.

Much of the increase in population density we observed was through the recruitment of juvenile immigrants. Juvenile red squirrels disperse in autumn and require a suitable territory to overwinter successfully (Kemp & Keith 1970; Rusch & Reeder 1978). It appears that the supplemental food we provided created favourable habitat as more animals investigated the area (newcomers) and were able to settle (recruits). Although the scale of the food addition areas (13 ha) may appear artificially small, natural cone crops are often very patchy, depending on local and regional conditions, and are not synchronous between species (Eremko, Edwards & Wallinger 1989). To cope with such a patchy environment, red squirrel movements may distribute animals in relation to changing resources (Taylor & Taylor 1977, 1983).

Recruitment to the food-supplemented areas and the decline in density after feeding ended were both density-dependent. Several studies have shown that small mammal populations are regulated by the exclusion of juveniles from the breeding population (see Sinclair 1989, for a summary). Territorial space may be regulating these populations, but as noted by Sinclair (1989), it is difficult to separate these results from interference competition for food if food availability is not known. We provided excess supplemental food in a regular pattern such that there were always more than two feeders on even the smallest territories. This pattern would make it difficult for individuals to monopolize access to a single large feeder (Ewald & Carpenter 1978; Monaghan & Metcalfe 1985) and hence, the decline in the recruitment rate with increasing density indicates that another factor is limiting the population at this higher density. Preliminary analyses indicate that territorial behaviour may be one of the factors which limits and regulates the population in the presence of abundant food (W. Klenner, unpubl.). In fir habitat, territory size decreased when supplemental food was added but only to the level observed in spruce habitat. The limited flexibility in territory size along with an increase in the proportion of time spent on territorial defence appeared to prevent newcomers from settling, even though excess food remained. Boag & Schroeder (1987) reported that more than one factor limited spruce grouse populations; spacing behaviour limited breeding density only in years when the population density was higher than average.

When supplemental feeding ended, squirrel populations on the food treatment areas declined to control levels over a 6-month period. Although the average rate of decrease was highest on the fir treatment areas, the monthly rate of change did not follow a clear density-dependent pattern. We believe that this can be attributed to the caching of seed and the lack of alternative, suitable territories after the onset of winter. To survive the winter, red squirrels require a cache of stored food (C. Smith 1968; M. Smith 1968; Kemp & Keith 1970) and the length of time that squirrels stayed after supplemental food was removed may be related to the size of their food caches.

We expected body weights to increase when supplemental food was added since Wauters & Dhondt (1989) reported that both survival and fertility were positively correlated with body weight of red squirrels (*Sciurus vulgaris*) in Belgium. We observed little change in body weight, either at the population or individual level. Other food addition studies have demonstrated an increase in body weight and growth rates in response to supplemental food (see Boutin 1990 for a review). Red squirrels rely largely on their food cache as an overwinter food supply (Kemp & Keith 1970; Rusch & Reeder 1978) and may not require large body fat reserves, thereby avoiding the increased costs of locomotion associated with greater body mass (Trombulak 1989).

Despite the lack of a consistent pattern of changes in body weight, survival, reproduction and sex ratio, food availability may influence these parameters in red squirrels. The period when supplemental food was available may have been too brief to affect the animals, or the magnitude of the change may have been too small to detect with the low number of replicates in our sample. The area which received supplemental food was large enough to allow detection of population changes but the physiological responses of individuals may have lagged (Price 1986; Wiens, Rotenberry & Van Horne 1986). It is interesting to note that after the large cone crop in spruce habitat in 1985, females reached breeding condition at least 1 month earlier in 1986 than in subsequent years. By breeding early, females may be able to enhance the chances of their offspring obtaining a territory. For example, juveniles from early litters would encounter more vacant territories (due to cumulative overwinter mortality) during dispersal than juveniles weaned in late summer. Also, we did not measure litter size. This shortcoming could be overcome by providing nestboxes and monitoring litter size and offspring survival to weaning.

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