THE EFFECT OF FOOD ABUNDANCE AND TERRITORIAL BEHAVIOUR ON POPULATION DYNAMICS OF THE RED SQUIRREL

by

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ABSTRACT

The effects of food abundance on the population dynamics and territorial behaviour of red squirrels were examined during a four year study in south-central British Columbia, Canada. I used a short-term, *ad libitum* addition of supplemental food in Douglas fir (low squirrel population density) and white spruce (high squirrel population density) forest habitats to examine changes in demography and spacing behaviour. Removal experiments in spring and autumn assessed the effect of residents on breeding density and juvenile recruitment and the influence of settlement patterns on recolonization density.

If food is a limiting resource, I expected population density, recruitment, body weight, growth rates and reproduction to increase on the food supplemented areas. Population density in spruce control habitat was consistently twice as high as in Douglas fir control habitat (26 vs. 15) from 1985 to 1988. The addition of supplemental food resulted in a four-fold increase in population density in Douglas fir habitat and a two-fold increase in spruce habitat, indicating that populations in both habitats were food limited, but more strongly in Douglas fir habitat. The increase in density was the result of a strong increase in the recruitment of immigrants, primarily juveniles of unknown origin. Both recruitment to the food-supplemented grids and the decline in density following the removal of food were density-dependent.

Stable population density may be the result of an inflexible territory size despite large changes in food abundance. To test this hypothesis, I monitored changes in territory size, home range size, the number of territories, intruder pressure, movement patterns and activity budgets in response to supplemental food. Supplemental food significantly decreased territory size and resulted in a five-fold increase in the number of territories in Douglas fir habitat. Territory size did not decrease in white spruce habitat, but there was a two-fold increase in the number of territories. In both habitats, immigrants established territories in previously unoccupied areas and in Douglas fir
habitat, some immigrants established small territories on areas formerly used by residents who had defended large territories. There was an increase in the intensity that red squirrels travelled over their territories, a decrease in the proportion of time spent away from their territories and an increase in the proportion of time spent defending their territories. These behavioural changes appeared to offset the increased competitor density on the enriched territories, enabling red squirrels to defend territories larger than necessary for their current food requirements. This limited flexibility in territory size may reduce the amplitude of fluctuations in population density despite large changes in food abundance.

Territorial behaviour can limit breeding density and juvenile recruitment. When territorial residents were removed from Douglas fir habitat in spring, red squirrel populations returned to a density similar to the control or pre-removal density in five of six removal trials. In autumn, population density returned to control or pre-removal densities in four of six trials. In white spruce habitat, population density returned to control or pre-removal levels in three of four trials in both spring and autumn. In both Douglas fir and spruce habitat, immigrants of unknown origin repopulated the removal areas. After removals in spring, females in breeding condition immigrated to the removal areas in five of six trials in Douglas fir habitat and in all four trials in spruce habitat. Settlement patterns did not appear to influence either territory size or recolonization density.
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Chapter 1

GENERAL INTRODUCTION

Territorial behaviour can influence population size by limiting breeding density. In 1970, Watson & Moss outlined four criteria which they argued must be met to demonstrate that territorial behaviour limits breeding density: (1) that potential breeders are excluded by territorial residents, (2) that these non-breeders can breed if given the opportunity, (3) that some other resource such as food or nest sites is not limiting, and (4) that the mortality or reduced recruitment due to spacing behaviour is inversely proportional to other forms of mortality. Hannon (1983) indicated that for conditions one and two to be valid, members of the limiting sex must be prevented from breeding. Smith & Arcese (1986) and Smith, Arcese & Hochachka (in press) suggested two further conditions to show that territorial behaviour limits total population size: (1) that both the number and proportion of non-territorial animals in the population should be related to the density of territory holders, and (2) that the fate of all animals in the population is known. Although the role of territorial behaviour in regulating animal populations has received widespread support (Wynne-Edwards 1962; Brown 1969; Watson & Moss 1970; Carl 1971; Patterson 1980), there is considerable debate over whether spacing behaviour or other factors limit breeding density and population size (Krebs 1971; Dunford 1977; Bergerud & Butler 1987; Boag & Schroeder 1987; Hannon & Zwickel 1987; Smith, Arcese & Hochachka in press).

There is little doubt that food can ultimately limit population size, the main controversy being whether populations ever reach this limit (Newton 1980). Lack (1954; 1966) did not subscribe to the view that territorial behaviour limits breeding density, but supported the view that food abundance and overwinter mortality limit breeding density and that territorial behaviour serves primarily to space out individuals within the available habitat. Food can régulate animal populations through competition for this
resource and has been shown to regulate several species, primarily large mammals (Sinclair 1989). While much circumstantial evidence has been offered for the effect of food on population dynamics, the strongest evidence for the role of food on demography comes from experimental manipulations (Newton 1980; Martin 1987; Boutin 1990).

Although most studies have examined the influence of food or territorial behaviour in isolation, there is an increasing need to look at the interactions among two or more factors (Hilborn & Stearns 1982; Sinclair 1989). For example, territorial behaviour may appear to regulate population density, but if territory size varies with food abundance, then competition for food is the regulating factor and territorial behaviour simply determines which animals can exploit the resource. This may be a common and realistic situation since territoriality depends on and has probably evolved in response to the distribution and quality of food (Brown 1964; Gill & Wolf 1975; Smith, Arcese & Hochachka in press). Also, food abundance may enhance the effect of predation by increasing the vulnerability of prey (Keith et al. 1984).

The relationship between territorial behaviour and intrinsic (Chitty 1967; Krebs 1985) or extrinsic factors such as food abundance is not well understood. Increased food abundance often leads to decreased territory or home range size (see Boutin 1990 for a review). For example, migratory hummingbirds defend territories which can change size on a daily basis as food availability changes (Gass, Angehr & Centa 1976; Kodrick-Brown & Brown 1978). In contrast, some long-lived species (Southern 1970; Von Schantz 1984b) apparently defend territories of fixed size despite large changes in food abundance. To complicate the relationship between food abundance and territory size, other factors such as settlement patterns have also been shown to influence territory size (Van den Assem 1967, Zahavi 1971).
Study animal

The red squirrel (*Tamiasciurus hudsonicus* Erxleben) is a small arboreal sciurid found throughout the boreal forests of North America. Red squirrels defend sex-specific territories (C. Smith 1968; Kemp & Keith 1970; Rusch & Reeder 1978) except during the brief mating season in spring when males travel widely and are tolerated on female territories. Although red squirrels appear to be strongly territorial across much of their range, some populations in eastern deciduous forests may not be (Layne 1954). In coniferous forests, cones are the primary overwinter food and territories are defended throughout the year. Each territory may have one or more caches of stored cones (middens) from a previous large cone crop and these may remain available for several years without spoiling (C. Smith 1968; M. Smith 1968; Kemp & Keith 1970; Gurnell 1984). During summer, squirrels feed on a wide range of foods including the cambium of coniferous trees, fungi and berries. Cones ripen in late July and are either eaten in the trees or clipped from branches and later stored in the midden. The number of cones produced each year varies greatly (Eremko, Edwards & Wallinger 1989), and storing cones appears to be a way of averaging these fluctuations. Offspring are usually born between April and June, and in central British Columbia there is only one litter per year (Millar 1970). The young are weaned between July and September and then either disperse or establish residence within their mother's territory (C. Smith 1968; Boutin & Schweiger 1988).

Red squirrels are an ideal species on which to conduct studies of the relationship between food, territorial behaviour and population dynamics. Unlike most mammals, red squirrels are diurnal, they defend their territories with conspicuous calls and they soon habituate to observers. Food abundance can be manipulated easily by adding supplemental food such as seeds. Since red squirrels defend sex-specific territories, have
only one litter per year and mature as yearlings, the relationships between individuals in the population are relatively simple.

Objectives and organization of the thesis

In this thesis, I examine the effect of food abundance and territorial behaviour on the population dynamics of the red squirrel. I had four main objectives: (1) to evaluate the effect of increased food abundance on red squirrel demography in good and poor quality habitat (high and low squirrel population density), (2) to examine the effect of changing food abundance on territory size and behaviour, (3) to determine if territorial behaviour limits breeding density and juvenile recruitment, and (4) to examine the effects of settlement patterns on the territory size and density of recolonizing squirrels.

In chapter 2, I present the results of a food addition experiment to examine the effect of changing food abundance on demography. I test the hypothesis that red squirrel populations are limited by food and examine how populations in good and poor habitat respond to excess, high quality food.

In chapter 3, I focus specifically on the effects of supplemental food on territory size and behaviour, and test the hypothesis that red squirrels defend territories of fixed size despite large changes in food abundance. I monitor changes in territory size directly by observing colour marked or radio-transmitter equipped squirrels and examine the behavioural changes which occur as the density of competitors increases.

In chapter 4, I evaluate the role of territorial behaviour in limiting breeding density and juvenile recruitment. I use removal experiments to test the hypothesis that there are surplus potential breeders in the population in spring and surplus juveniles in autumn which have not been able to establish themselves because of territorial behaviour by residents. I also examine the influence of settlement patterns on recolonization density by conducting the above removals either simultaneously or asynchronously. I tested the hypothesis that simultaneous settlement leads to higher recolonization density.
and a smaller territory size by: (1) comparing density on simultaneous and asynchronous removal areas with control populations, (2) documenting changes in territory size after removing animals simultaneously, and (3) comparing the change in density of food supplemented populations where residents were either removed or left in place before adding food.
Chapter 2

THE EFFECT OF SUPPLEMENTAL FOOD ON RED SQUIRREL POPULATION DYNAMICS

INTRODUCTION

Two critical questions concerning animal abundance are: what causes differences in population density between habitats; and what influences density within a specific habitat (Chitty 1960). Food availability has long been recognised 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 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 and Sullivan (1982) noted a positive response to the addition of supplemental food in the closely related Douglas squirrel (Tamiasciurus douglasii). However, the use of trapping lines made estimates of changes in density tenuous. In a subsequent investigation, Sullivan (in press) found that the population density of red squirrels did increase during a long-term feeding study.
Food addition studies on a number of small mammal species including *Peromyscus maniculatus* (Gilbert & Krebs 1981, Taitt 1981), *Microtus townsendii* (Taitt & Krebs 1981), *Lepus americanus* (Krebs et al. 1986) and *Spermophilus columbianus* (Dobson and Kjelgaard 1985) all indicate a positive demographic response to supplemental food. Differences between the above studies and the predictions of Rusch & Reeder (1978) may be related to the long-term stability of red squirrel territories. In a study of the tawny owl (*Strix aluco*), Southern (1970) reported stable populations of adults despite large fluctuations in the food supply. To explain the apparent stability of a red fox (*Vulpes vulpes*) population, Von Schantz (1984a, b) described a conceptual model which incorporated individual longevity and fluctuations in food availability. Stable populations resulted from inflexible territory boundaries which obviate the need to evict neighbours as food availability decreased.

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 chapter, I describe the effect of adding a short-term provision (pulse) 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. I 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, I predicted that population density should rise to that level. If food limits population size, I also predicted that body weight, growth rate, survival and reproduction would increase.

I used a pulsed 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 I 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, I was 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
mean annual precipitation of 40 cm. Predominant coniferous overstory 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 overstory
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 and Coupe (1979).

**Experimental design**

Eight study plots were established in Douglas fir and white spruce habitat
between 1985 and 1987. In Douglas fir habitat, a replicated design (2 control, 2 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 x 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 (8x12, 7x14, 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. I placed traps at every second station on the grid, resulting in approximately five traps per hectare. Squirrel populations were censused by live-trapping every 3-5 weeks during April to December and every 6-8 weeks during January to 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 to March) necessitated irregular trapping during this period.

During trapping sessions, traps were set for two days and were checked three times. Traps were opened shortly after dawn on the first day, checked four hours 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 ear tags for individual identification at subsequent captures or when squirrels were observed foraging. When squirrels were captured, I recorded the ear tag number, location, weight (to ± 5 g on a Pesola spring-balance), sex and breeding condition. I 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 testes were 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, I
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). 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. Since the JS and MNA estimates
indicated a similar pattern of population change, I used the JS estimate to compare
differences in trappability, population size and survival. I used the more conservative
MNA estimate (Jolly and Dickson 1983; Krebs & Boonstra 1984) to examine recruitment
in relation to population density to avoid inflated estimates of population size resulting
from the large number of newcomers (see below) captured on the food addition areas.

I 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 (Chapter 3). To compare recruitment between treatments, I averaged the 1986 and 1987 live-trapping data. I 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. The minimum length of the breeding season was calculated as the number of weeks during which a female was observed lactating. The maximum length was estimated as the minimum length plus three-quarters of the time to the previous and next trapping session. Because of the relatively long interval between trapping sessions (3 to 4 weeks), the maximum length was used to estimate the breeding season of squirrels which may have come into breeding condition shortly after or just prior to a trapping session.

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. The difference in the length of time that supplemental food was available in the two habitats was the result of logistic constraints associated with assessing territory size (Chapter 3). These differences should not influence the results of the experiment since there was little increase in density after the first six weeks of supplemental food. When each pulse of supplemental food 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 three months. Sunflower seed was distributed in five litre plastic pails which were attached to large trees and sheltered from rain with a cover (30 x 30 cm). Feeders were located approximately 2 m above ground in a 12 x 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 44 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 several consecutive trapping sessions), I 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, I averaged the JS density estimates from three trapping periods before food was added, when it was present and during the period six to eight months after the end of the food addition. I used a t-test to examine these localized differences in density between control and treatment grids. To evaluate differences between treatments within a period, I used a one-way ANOVA and the Tukey HSD multiple comparisons test to examine differences between means if results of the ANOVA indicated significant differences. When the probability for a multiple comparisons test is given, it represents the highest value for a particular set
of comparisons. 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 were repeated in 1986 and 1987, the data were combined and the mean value 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 $\alpha = 0.05$.

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 desireable food. When squirrels emerged from their nests at dawn, they would often feed on sunflower seeds at a feeder for 5 - 10 minutes 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

I calculated the overall trappability of juveniles and adults as well as trappability during the period when supplemental food was available (Table 2.1). The trappability of juveniles was always greater than the trappability of adults (average of 94 % across all treatments vs. 72 % for adults). The overall trappability of juveniles in Douglas fir control habitat (91 %) was less than in spruce control habitat (99 %) (Tukey HSD, $P = 0.032$). During the food addition period, juveniles in Douglas fir control habitat were again less trappable (83 %) than juveniles in spruce control habitat (98 %). In neither Douglas fir nor spruce habitat did the addition of supplemental food affect the trappability of either juveniles or adults ($P > 0.15$).
**Population density**

The addition of supplemental food increased population density in both Douglas fir and spruce habitats (Fig. 2.1). Although the change in density in Douglas fir habitat was greater than in spruce habitat (4.1-fold vs. 2.1-fold), populations in both habitats reached approximately the same average density. A repeated-measures ANOVA indicated that in Douglas fir habitat, the overall food effect was significant \((P = 0.039)\) while the time (trapping period) and food by time interaction effects were both highly significant \((P < 0.001)\). In spruce habitat, the results were similar except that the food by time interaction was not significant \((P = 0.335)\).

I 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 Douglas fir habitat, control and treatment grids were not significantly different before supplemental food was added in 1986 or 1987 (May to July) \((t=1.31, df=2, P = 0.321; t=2.76, df=2, P = 0.11\) respectively). While supplemental food was present (August to early November), the control and food grids were different in 1986 but not in 1987 \((t=17.76, df=2, P = 0.003; t=3.01, df=2, P = 0.095,\) respectively). In spruce habitat, control and treatment grids were not different before supplemental food was added (May to 20 July, 1987) \((t=0.35, df=2, P = 0.759)\). While supplemental food was present (21 July to 20 October, 1987), control and food treatments were significantly different \((t=3.92, df=2, P = 0.034)\). In 1986, the control and treatment grids showed the same trend as in 1987 (Fig. 2.1).

**Body weight and growth rate**

There were no consistent differences in mean adult body weight between the control and food treatments in either Douglas fir or spruce habitat. When averaged
Figure 2.1. 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.
Table 2.1. Estimates of Jolly trappability (mean ± 1 S.E.) for juvenile and adult red squirrels. Values are mean percent trappability (number caught / Jolly-Seber population estimate x 100) and are based on the mean of two replicates for each treatment.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Juveniles</th>
<th>Adults</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total¹</td>
<td>Food²</td>
</tr>
<tr>
<td>Fir Control</td>
<td>90.9 (0.8)</td>
<td>83.1 (4.2)</td>
</tr>
<tr>
<td>Fir Treatment</td>
<td>92.3 (0.6)</td>
<td>87.3 (0.8)</td>
</tr>
<tr>
<td>Spruce Control</td>
<td>99.2 (0.8)</td>
<td>97.8 (2.2)</td>
</tr>
<tr>
<td>Spruce Treatment</td>
<td>96.1 (1.0)</td>
<td>93.5 (2.0)</td>
</tr>
</tbody>
</table>

¹ Represents trappability during entire period of study.

² Represents trappability during the two periods (1986 and 1987) when supplemental food was available on the treatment grids.
across the three years of live trapping, the weights of both adult males and females in Douglas 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, I noted the same pattern between control and treatment areas (males: 220.8 vs 224.6 g; females: 211.1 vs 212.8 g, respectively). Adult males and females weighed approximately the same in Douglas fir habitat but in spruce, males tended to be approximately 10 g heavier than females (222.7 vs. 212.0 g). The pulse of supplemental food did not have a clear effect on mean body weights, either while food was present or after feeding was discontinued.

Juvenile body weights in control and food supplemented areas did not differ consistently in either Douglas fir or spruce habitat. In the first trapping period in 1986, juveniles in Douglas fir control habitat, on average, weighed 30 g less than juveniles in Douglas fir treatment habitat but this pattern was not repeated in 1987.

To determine if changes in the body weights of certain individuals were being masked by looking at the mean body weight of all animals captured, I examined the changes in body weight of randomly selected individuals. Again, there were no clear differences in adult body weight or rate of weight loss overwinter by adults between control and food-supplemented animals. Juveniles showed a similar pattern in both Douglas fir and spruce habitat. In comparing juvenile body weights, the low number of juveniles recruiting into control habitat made comparisons tenuous.

I examined the growth rates of juveniles in Douglas fir and spruce habitat by plotting the change in mean body weight over time. In 1986, juvenile males from the food addition areas in Douglas 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, there were no consistent differences in juvenile male growth rates between treatments in 1986 or 1987. Juvenile females from the food addition areas appeared to reach a higher body weight in the winter of 1987 (208 g vs. 194 g). Again, because of the low number of recruits in control habitat (one to three animals), these results must be interpreted with caution.

**Recruitment and population decline**

The addition of supplemental food had a strong positive effect on recruitment in both Douglas fir and spruce habitat. I was 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. 2.2) increased to an average of twenty-five during the second trapping period when supplemental food was available. In both Douglas fir and spruce control habitat, an average of eight newcomers were captured during this period.

The number of recruits also increased (Fig. 2.3). The apparent lag in recruitment which continued after the food addition ended is an artifact of how I 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, I 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, I assigned individuals which became recruits to the trapping period when they were first captured. The number of recruits did not differ between control and food grids, either before food was added (\( P > 0.52 \)) or after it was removed (\( P > 0.10 \)). While supplemental food was present, the number of newcomers and recruits greatly increased in both Douglas fir and spruce habitat (Tukey HSD, \( P < 0.006 \) in all comparisons between control and food). The proportion of male and female juveniles which established themselves as recruits was
Figure 2.2. 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.
Figure 2.3. 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.
similar. 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%).

I 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, I considered recruitment only on the food treatment grids to avoid confounding food availability and density effects. In both Douglas fir and spruce habitat, the recruitment rate was density-dependent (Fig. 2.4a, 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. 2.4b, d). Newcomers were present in both Douglas fir and spruce habitat during the three trapping sessions when supplemental food was available (Fig. 2.2). 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. I 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. Body weight, pelage condition and incidence of wounds were similar between these types of animals. Newcomers often attempted to claim "vacant" territories while the resident was in a trap, but were evicted upon release of the territory owner.

During the seven month period after supplemental feeding ended each year, the rate of population decline was greatest in Douglas fir treatment habitat (Table 2.2; Tukey HSD, $P < 0.023$). In Douglas fir treatment habitat, population density decreased at seven times the rate in Douglas fir control habitat and over twice the rate in either spruce habitat. The rate of population decline in Douglas fir control, spruce control and spruce treatment habitat was not significantly different ($P > 0.328$). Although the average rate of population decrease was greatest in the Douglas fir treatment areas, the monthly decline did not follow a clear density-dependent pattern (Fig. 2.5).
Figure 2.4. 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. (●) indicates replicate # 1, (■) replicate # 2. Dotted lines indicate trends as estimated by least squares regression.
Figure 2.5. 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 seven month period after supplemental feeding was discontinued. Dotted lines indicate trends as estimated by least squares regression.
Table 2.2. Mean monthly instantaneous rate of population change (± 1 S.E.) on control and food treatment areas during the seven month period after supplemental feeding was discontinued.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Rate of change$^1$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fir Control</td>
<td>-0.035 (1.50 x 10^{-4})</td>
</tr>
<tr>
<td>Fir Treatment</td>
<td>-0.250 (0.017)</td>
</tr>
<tr>
<td>Spruce Control</td>
<td>-0.052 (0.002)</td>
</tr>
<tr>
<td>Spruce Treatment</td>
<td>-0.118 (0.057)</td>
</tr>
</tbody>
</table>

$^1$ 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.
Table 2.3. 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.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Food(^1)</th>
<th>Post-Food(^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fir</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>0.52 (0.02)</td>
<td>0.92 (0.03)</td>
</tr>
<tr>
<td>Treatment</td>
<td>0.81 (0.04)</td>
<td>0.75 (0.03)</td>
</tr>
<tr>
<td>Spruce</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>0.68 (0.01)</td>
<td>0.90 (0.03)</td>
</tr>
<tr>
<td>Treatment</td>
<td>0.67 (0.03)</td>
<td>0.83 (0.06)</td>
</tr>
</tbody>
</table>

\(^1\) Juvenile survival during the three month period when supplemental food was available.

\(^2\) Juvenile survival during the five month period after supplemental feeding was discontinued.
**Survival**

I calculated juvenile Jolly survival (losses were due to both deaths and emigration) during the time when supplemental food was available and during the five month period after feeding was discontinued (Table 2.3). While supplemental food was available, juvenile survival on the Douglas fir control grids was lower than on the other treatments (Tukey HSD, $P < 0.046$). Survival was best on the Douglas fir treatment grids (0.81 per month) and intermediate on the spruce control and spruce food treatments (0.68 and 0.67 respectively). There were no significant differences in survival between either of the treatments after supplemental feeding was discontinued ($P > 0.125$), but survival on the Douglas fir control and spruce control areas was now higher than on the respective food treatment grids.

The decline in density on the food supplemented areas in late winter may be the result of *in situ* mortality (i.e. 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 I 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, I began to capture animals from the treatment grids on the adjacent control areas (approximately 1 km away). In the spring of 1987 and 1988, I caught nineteen squirrels which had moved from the treatment to the control grids. Of these, five eventually became permanent residents (four of fifteen in Douglas 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.

Supplemental food had little effect on adult survival. There were no significant differences in average adult survival between control and treatment areas either before (86% vs. 87%), during (95% vs. 90%), or after (94% vs. 92%) the addition of
supplemental food ($P > 0.15$). During the food addition period, adults in Douglas fir treatment habitat survived less well (85% per month) than in other areas (Douglas fir control, 94%; spruce control, 95%; spruce food, 94%) but the difference was not significant ($P > 0.12$). There was no difference in survival between males and females ($P > 0.30$).

Breeding

In Douglas fir habitat, 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 and spring. In 1986, adult males in Douglas fir treatment habitat remained scrotal for three weeks longer but this was before supplemental food was added, indicating high variability between years. Adult females reached breeding condition one month earlier in 1988 on one of the food addition areas but this pattern was not consistent across the two replicates. Yearling females on the food addition areas came into breeding condition about one month earlier than on the control areas in both 1987 and 1988.

In 1986, adult females in spruce habitat came into breeding condition at least one month earlier than in 1987 or 1988, but this was before supplemental food was added. I also captured a large juvenile (160 g) in spruce habitat on 25 May and several others in early June in 1986. From observations of known aged animals (young tagged in nest shortly after birth, unpublished data), I estimated that these animals would have been born between 15 April and 1 May. In other years, squirrels were usually born in early June. There was no difference in the proportion of adults in breeding condition in 1987 but in 1988, a slightly greater proportion (100% vs. 88%) of adults bred on the food addition areas. There were no clear differences in juvenile breeding but comparisons are tenuous because few juvenile females were captured in spruce control habitat.
Supplemental food had no measurable effect on the length of the breeding season as estimated by the number of weeks females were pregnant or lactating. From 1986 to 1988, the minimum length of the breeding season ranged from 4.0 to 10.0 weeks ($\bar{x} = 5.5$) across all treatments. The maximum length of the breeding season ranged from 6.0 to 15.3 weeks ($\bar{x} = 9.7$). I found no indication that females gave birth to a second litter on the food supplemented areas. Although the period during which obviously pregnant or lactating females were observed sometimes exceeded four months, no individuals were pregnant or lactating for more than 10 weeks. This period would be too short for an individual to give birth and wean two litters. Juveniles were usually nursed by the female for approximately 5 weeks before weaning (unpublished data). Also, I observed no females which had two periods of lactation, including animals which had apparently lost their litters shortly after parturition.

**Sex ratios**

Supplemental food did not appear to affect the sex ratio of adults (proportion of males) in either spruce or Douglas fir habitat ($\bar{x} = 0.52; P > 0.84$). Similarly, there was no difference in the sex ratio of juvenile newcomers or recruits ($\bar{x} = 0.53, P > 0.80; \bar{x} = 0.55, P > 0.24$, respectively).

**DISCUSSION**

**Population density**

In response to supplemental food, the average population density of red squirrels in both Douglas fir and spruce habitat increased to approximately the same level. The initial density in Douglas fir habitat was lower, and hence the four-fold increase there was greater than the two-fold 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 such as territorial behaviour (Chapter 3) may have 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 (in press). 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.). Gregory, Lacki & Williams (1988) noted that only female eastern chipmunks responded to additional food.

In contrast, Havera & Nixon (1980) found that supplemental feeding had little effect on gray 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 little evidence that the laboratory mouse chow provided was utilised. 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 Douglas 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 six weeks of the food addition by tearing feeder pails from
trees. Although the bears consumed some of the sunflower seed, I believe that the lesser 
response that I 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 then on either of the controls.

During 1986 and 1987, cone crops were light to moderate in both Douglas fir and 
spruce habitat (Table 2.4). The only large cone crop I observed was in white spruce 
habitat in 1985. I noted large cone crops on individual trees or small groups of trees (less 
than five) in both Douglas fir and spruce habitat during 1986 to 1988, but this was not as 
extensive as in 1985. Since my food addition experiments followed the large spruce cone 
crop in 1985, my results provide little insight into whether red squirrels are limited by 
food when cone mast is abundant. However, I would predict that squirrels are not limited 
by food availability during these years.

Recruitment and population decline

Much of the increase in population density I 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 I provided created favorable 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 and 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
Table 2.4. Estimates of cone crop abundance in Douglas fir and white spruce habitat.

<table>
<thead>
<tr>
<th>Year</th>
<th>Douglas Fir</th>
<th>White Spruce</th>
</tr>
</thead>
<tbody>
<tr>
<td>1985</td>
<td>Very light</td>
<td>Very heavy</td>
</tr>
<tr>
<td>1986</td>
<td>Light</td>
<td>Light</td>
</tr>
<tr>
<td>1987</td>
<td>Light-moderate</td>
<td>Light</td>
</tr>
<tr>
<td>1988</td>
<td>Light</td>
<td>Light</td>
</tr>
</tbody>
</table>

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. I provided excess supplemental food in a regular pattern so that individuals could not monopolize access to a single large feeder (Ewald & Carpenter 1978; Monaghan & Metcalfe 1985), hence, the decline in the recruitment rate with increasing density indicates that another factor is limiting the population at this higher density. Territorial behaviour may be one of the factors which limits and regulates the population in the presence of abundant food (Chapter 3). Boag & Schroeder (1987) reported that more than one factor appears to limit 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 six-month period. Although the average rate of decrease was highest on the Douglas fir treatment areas, the monthly rate of change did not follow a clear density-dependent pattern. I 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). The length of time that squirrels stayed after supplemental food was removed may be related to the size of their food caches. I was not able to quantify the amount of food stored in caches, but this may explain why some squirrels left the area in February while others did not leave until late June.

**Body weight, survival and reproduction**

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
influence the animals, the time of year may have been inappropriate, or the magnitude of
the change may have been too small to detect with the low number of replicates in my
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
one 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 born litters would encounter more vacant territories during dispersal
(due to cumulative overwinter mortality) than juveniles weaned in late summer. Also, I
did not measure litter size. This shortcoming could be overcome by providing nestboxes
and monitoring litter size and offspring survival to weaning.

I 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. I 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 (Desy & Thompson 1983, Dobson & Kjelgaard 1985, also
see Boutin 1990 for a review). An increase in body weight in the present study may have
been offset by the higher energetic demands of defending the territory against intruders
on the food addition areas (Chapter 3).
Chapter 3

THE EFFECT OF SUPPLEMENTAL FOOD ON RED SQUIRREL BEHAVIOUR

INTRODUCTION

Several studies have examined the response of animal populations to changes in food abundance through the use of experimental food additions (Taitt 1981; Taitt & Krebs 1981; Mares et al. 1982; Desy & Thompson 1983; Watson, Moss & Parr 1984; Dobson & Kjelgaard 1985; Krebs et al. 1986; also see Boutin 1990 for a review). Much of this work has focused on whether a population is limited by food and what demographic parameters are affected. Supplemental food usually increases density, advances breeding and occasionally increases litter size (Boutin 1990). In a review of several food addition experiments, Gilbert & Krebs (1981) suggested that a two to three-fold increase in density is normal when excess supplemental food is added, and that research should focus on why the response is not greater.

Spacing behaviour may be one factor which limits population responses to supplemental food. The potential regulatory effect of territorial behaviour on local population density was noted by Brown (1969) and Watson and Moss (1970), and mathematical models have shown that differences in resource partitioning between individuals (Lomnicki 1980) or inflexible spacing behaviour (Stenseth 1985) can stabilize population density. If territorial behaviour affects population density, then the factors which affect territory size will also influence density (Hixon, Carpenter & Paton 1983).

Southern (1970) suggested that territory size may remain fixed in some long-lived species despite large changes in food availability. Alternatively, Patterson (1980) brought together the ideas of economic defendability developed by Brown (1964) and others (Charnov, Orians & Hyatt 1976; Davies 1978; Gill & Wolf 1978) and proposed that territory size varies in response to changes in resources such that density is adjusted
to variations in the environment. This hypothesis is supported by studies on both migratory (Gass, Angehr & Centa 1976; Kodrick-Brown & Brown 1978) and overwintering species of birds (Enoksson & Nilsson 1983) and has been called the multifactor resource-behaviour hypothesis (Sinclair 1986). Patterson's (1980) resource-behaviour hypothesis predicts that population numbers will fluctuate along with changes in food abundance. In contrast, Southern's (1970) hypothesis predicts that changing food abundance will not affect territory size and as a consequence, numbers will remain stable. In support of the Southern hypothesis, Kemp & Keith (1970) and Rusch & Reeder (1978) reported that red squirrels maintained a constant territory size despite fluctuations in food availability between years. They suggested that territory size was inflexible and was large enough to contain adequate food during years of low cone production.

I tested Southern's (1970) inflexible territory size hypothesis and Rusch & Reeder's (1978) conclusion that red squirrels defend territories of fixed size despite large changes in food resources by supplying replicate study areas in two habitat types with *ad libitum* supplemental food. I predicted that if the inflexible territory size model applies to red squirrels, territory size should not change despite changes in food abundance. In addition, I describe changes in intruder pressure, movement patterns, activity budgets and the intensity of territorial defence to examine the behavioural mechanisms which affect the use of space.

**METHODS**

*Study area*

Data on red squirrel behaviour were collected on eight study plots monitored in 1986 and 1987. Details of the study area, experimental design, supplemental food and statistical analyses are presented in Chapter 2.
Monitoring behaviour

Each plot was surveyed and marked with stakes placed at 15 m intervals in a square grid to facilitate recording the locations of animals. Around each study plot, a 120 m wide border strip was surveyed and marked with stakes to enable me to establish the locations of animals which foraged away from the central area. I monitored the territory size of squirrels in summer from 1 June to 10 August and in autumn from 20 August to 20 November. I recorded information on squirrel behaviour to help me distinguish between territories and home ranges. I delineated territory boundaries by recording the locations where squirrels displayed behaviours which discouraged intrusions by conspecifics (Burt 1943). Territorial behaviours included: (1) an aggressive screech call, (2) territory advertisement calls (the rattle call reported by C. Smith 1968, 1978), (3) the chasing of intruders, and (4) fights between residents and intruders. Home ranges were delineated by where squirrels travelled, irrespective of behaviour. Fights between neighbors were uncommon; during three years of observations, I observed less than ten actual fights. Territorial disputes were usually settled by long (up to 30 min), alternating exchanges of advertisement calls given from trees on opposite sides of what appeared to be a territory boundary.

To estimate territory and home range sizes, I used the 90% convex polygon estimate (Mohr 1947) to omit occasional excursions. I calculated the cumulative area as new locations were added to determine if an asymptote in territory area was reached (estimated visually) during the monitoring period (Mares, Willig & Bitar 1980; Voigt & Tinline 1980). Animals which were not monitored for a minimum of four hours over a one week period or which did not reach an asymptote were not included in subsequent analyses of territory size. This procedure excluded 72 of 140 resident squirrels during summer and 78 of 214 residents in autumn. For home range comparisons, only those animals with greater than twenty-five locations (most animals were located more than
seventy-five times) and which had reached an asymptote in cumulative area were included in the analyses.

During summer and autumn, I fitted selected animals with radio transmitters (Model SR-1, Biotrack, Stoborough, England) to allow me to track and identify individuals at a distance. Transmitters weighed approximately nine grams and emitted a frequency specific, pulsed signal in the 151.100 to 151.700 MHz range. Animals were equipped with transmitters on the basis of their residency on the study plot, the availability of transmitters and body weight. Juveniles weighing less than 160 g were not fitted with transmitters.

Each observer monitored from two-four animals daily. Squirrels were followed intensively during periods of peak activity (dawn to 1100 h, 1700 h to dusk) and intermittently during mid-day. Groups of animals were selected such that territorial interactions between individuals could be observed. Individuals were watched for approximately one hour before switching to a different focal animal. When an animal was being followed, data on the time and location of behaviours were recorded. Seven behaviours were recognized: territorial defence, feeding, foraging, caching food, resting, alert and mating behaviour. When food was added to the experimental plots, territory size was evaluated after supplemental food had been available for more than four weeks.

Spatial and behavioural analyses

I evaluated changes in spacing behaviour in response to the addition of supplemental food by comparing changes in territory and home range size. I estimated the number of territories on the central 9 ha of each grid by three methods: (1) during live-trapping, I observed animals when they were released from traps to determine if they exhibited territorial behaviour (e.g. gave territorial advertisement calls or chased intruders), (2) animals that were captured during three or more consecutive trapping sessions were considered to be territorial residents, and (3) from behavioural data
collected on animals equipped with radio transmitters or coloured ear tags. The above methods gave close agreement and any discrepancies were the result of assigning territorial status to animals that defended territories on the edge of the central 9 ha study plot.

I estimated changes in intruder pressure by recording the cumulative number of new (untagged) animals and total number of animals captured (averaged across 1986-87) during three live-trapping sessions before and during the time when supplemental food was available. The total number of animals captured during live-trapping included both new animals and residents in the estimate of intruder pressure. I used the number of animals captured as an estimate of intruder pressure since observers were inefficient at detecting intruders where there was dense undergrowth. The number of animals captured during live-trapping should not be affected by differences in vegetation between or within grids, but does include both animals which are attempting to establish territories (actual intruders) and transient animals. Since I could not distinguish the two types of animals, I considered all new animals captured as intruders which would settle if given the opportunity.

Movement patterns were assessed by calculating the distance moved per minute when an animal was active (i.e. when not sleeping or in a nest) and when sequential locations were less than 30 min apart. These criteria restricted the analyses to the data collected from focal animals and excluded repeated observations of inactive animals. As an indication of the level of territorial defence, I recorded the number of territorial advertisement calls that focal animals gave per hour while being monitored.

To evaluate whether squirrels spent a greater proportion of time on their territories during the food addition period, I calculated the proportion of home range locations which lay outside the territory boundaries. In 1987, I examined changes in amount of time spent on feeding, food caching, resting and territorial behaviour after supplemental food was added. Since I did not have detailed time budget information, I
used the proportion of observations which had each of the above behaviours as an estimate of the proportion of time spent on various behaviours. This analysis included only those locations where I was able to observe clearly the animal being monitored. Feeding behaviour included foraging for and consuming food on the ground or in trees. Food caching behaviour involved clipping cones from trees, moving food items to cache sites and caching food items in trees or in holes dug in the ground. Resting behaviour included time spent in the nest or midden, grooming and comfort activities and periods of sleep while in a tree. Territorial behaviour involved active defence of the territory through chasing intruders, fighting and giving advertisement or screech calls.

RESULTS

Changes in territory and home range size

Spatial analyses are based on 30382 observations of 248 individuals monitored over approximately 2000 h in 1986 and 1987. Feeding trials on red squirrels (unpublished data) indicated that animals ate approximately 70 g of whole sunflower seed per day in captivity (outdoors, ambient conditions, approximately 75 m³ cages) to survive and maintain body weight for two years. Although other small mammals and birds undoubtedly ate some of the sunflower seed during the food addition experiments, these animals did not restrict the squirrels' access to feeders. In addition to eating the supplemental food, squirrels in the wild continued to feed on cones and fungi even when ad libitum sunflower seed was present.

In both Douglas fir and spruce habitat, there was little difference in territory size on the control and treatment grids during summer (Table 3.1; \( P > 0.28 \)). However, territories in Douglas fir habitat (1.23 ha) were approximately three times as large as in spruce habitat (0.37 ha)(Figs. 3.1 and 3.2; Tukey HSD, \( P < 0.01 \)). During the autumn period, territories on the Douglas fir treatment grids were less than half the size of those
Figure 3.1. 90% convex polygon estimates of red squirrel territories in Douglas fir habitat in 1987. a) control, summer (1 June - 10 August), b) control, autumn (20 August - 20 November), c) treatment, summer, d) treatment, autumn. Large dots indicate the activity centers of territories for which sufficient locations were not available to delineate the territory (cumulative area did not reach an asymptote). Each polygon represents a different animal.
Figure 3.2. 90% convex polygon estimates of red squirrel territories in white spruce habitat in 1987. (a) control, summer (1 June - 10 August), (b) control, autumn (20 August - 20 October), c) treatment, summer (1 June - 10 August), d) treatment, autumn (20 August - 20 October). Large dots indicate the activity centers of territories for which sufficient locations were not available to delineate the territory (cumulative area did not reach an asymptote). Each polygon represents a different animal.
Table 3.1. Mean (± 1 S.E.) territory (ha) and home range size (ha) of red squirrels monitored during summer and autumn, 1986 and 1987. All areas are based on the mean of two replicates. Values in brackets indicate the number of territories or home ranges used to calculate the mean for each replicate.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Territory</th>
<th>Home Range</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Fir Control</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer</td>
<td>1.39 (0.12) [9,4]</td>
<td>4.76 (1.20) [9,4]</td>
</tr>
<tr>
<td>Autumn</td>
<td>0.55 (0.09) [9,2]</td>
<td>1.64 (0.03) [8,4]</td>
</tr>
<tr>
<td><strong>Fir Treatment</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer</td>
<td>1.07 (0.07) [8,6]</td>
<td>2.83 (0.68) [8,6]</td>
</tr>
<tr>
<td>Autumn</td>
<td>0.23 (0.06) [27,16]</td>
<td>0.54 (0.08) [26,16]</td>
</tr>
<tr>
<td><strong>Spruce Control</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer</td>
<td>0.38 (0.10) [17,5]</td>
<td>1.39 (0.59) [17,5]</td>
</tr>
<tr>
<td>Autumn</td>
<td>0.30 (0.01) [20,9]</td>
<td>0.57 (0.11) [20,9]</td>
</tr>
<tr>
<td><strong>Spruce Treatment</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer</td>
<td>0.36 (0.01) [15,4]</td>
<td>1.30 (0.24) [15,4]</td>
</tr>
<tr>
<td>Autumn</td>
<td>0.22 (0.05) [40,13]</td>
<td>0.39 (0.12) [39,13]</td>
</tr>
</tbody>
</table>
on the Douglas fir control grids (P = 0.056) and were now approximately the same size as territories in spruce habitat (P > 0.50). Despite the addition of supplemental food, territory size on the spruce treatment grids (0.22 ha) was approximately the same as in spruce control habitat (0.30 ha, P > 0.50). Mean territory size in autumn included adults that were present in summer and juveniles that began to establish territories in mid-August.

I used a paired t-test to compare changes in the territory size of adults that were present in summer and maintained territories during autumn (Table 3.2). On the Douglas fir control grids, there was a 60% decrease in territory size from summer to autumn (mean decrease = 0.92 ha, t=2.88, df=7, P = 0.03). Much of this difference can be attributed to two adult males which maintained exceptionally large territories during summer (2.47 and 2.45 ha, the largest of sixty-eight territories) and then defended territories of average size in autumn. The mean territory size of squirrels on the Douglas fir treatment grids decreased by 75% in response to supplemental food (mean decrease of 0.90 ha; t=6.23, df=10, P < 0.001). The changes in territory size on spruce control grids (mean increase of 0.01 ha) and on spruce treatment grids (mean decrease of 0.06 ha) from summer to autumn were both very small (P > 0.50, Fig. 3.2).

The mean territory sizes of juveniles were not different than those of adults in either Douglas fir (0.22 vs. 0.26 ha) or spruce (0.15 vs 0.25 ha) habitat during the food addition period on the treatment grids (P > 0.98, P > 0.74, respectively). These results further indicate that the decrease in territory size in Douglas fir treatment habitat involved a decrease in adult territory size and was not merely the result of an increase in the number of juveniles with small territories.

During summer, average home range size was larger but also more variable in Douglas fir habitat than in spruce (3.8 ha vs. 1.4 ha; P > 0.10). From summer to autumn, home range size decreased by more than 59% on all grids (Table 3.1) but the amount of the decrease was greatest in Douglas fir habitat where supplemental food was added
(81%). In autumn, home range size in Douglas fir control habitat was three times as large as in the other treatments (Tukey HSD, $P < 0.01$). Home range size in Douglas fir treatment habitat was not significantly different from home range size in spruce habitat ($P > 0.38$).

**Number of territories**

The number of territories on control grids in Douglas fir and spruce habitat changed little from 1986-88 (Fig. 3.3). In Douglas fir and spruce habitat, there was a five- and two-fold increase, respectively, in the number of territories when supplemental food was added. In 1986, the number of territories on the food treatment areas increased to an average of 25 per 9 ha and in 1987, the average increase was to 28 per 9 ha. In Douglas fir habitat, food treatment, time and treatment by time interaction effects were all significant (ANOVA, $P = 0.029$, $P < 0.001$, $P < 0.001$, respectively). In spruce habitat, the results were similar except that the overall food effect was no longer significant ($P = 0.235$). A significant food treatment by time interaction reflects a difference in the response of the control and treatment over time, indicating an increase in density on the food treatment grids.

The number of red squirrel territories increased while supplemental food was present in both Douglas fir and spruce habitat, and then declined to control levels by the following June. In Douglas fir habitat, there were more territories on the treatment grids while supplemental food was present in both 1986 and 1987 ($t=4.767, df=2, P = 0.041$; and $t=10.36, df=2, P = 0.009$, respectively). By the next June, these differences were no longer significant ($t=1.972, df=2, P = 0.187$; $t=0.902, df=2, P = 0.462$ in 1986 and 1987, respectively). In spruce habitat, supplemental food resulted in a significant increase in the number of territories in 1987 ($t=4.982, df=2, P = 0.038$). As in Douglas fir habitat, the number of territories declined to control levels by the following June ($t=0.845, df=2, P = 0.487$).
Figure 3.3. Number of territories on each 9 ha study plot in (a) Douglas fir and, (b) white spruce habitat from 1986 to 1988. (○) and (□) represent controls, (●) and (■) represent food addition treatments. Shaded area indicates the period during which supplemental food was available.
Table 3.2. Mean (± 1 S.E.) territory size of adult red squirrels present in both summer and autumn and juveniles present in autumn. Territory size expressed as hectares and is based on the mean territory size from each of two replicates, 1986 and 1987 data combined.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Summer</th>
<th>Autumn</th>
<th></th>
<th>Autumn</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Resident Adults</td>
<td>n</td>
<td>All Adults</td>
<td>Juveniles</td>
</tr>
<tr>
<td>Fir Control</td>
<td>1.55(0.31)</td>
<td>0.63(0.04)</td>
<td>7</td>
<td>0.66(0.04)</td>
</tr>
<tr>
<td>Fir Treatment</td>
<td>1.21(0.15)</td>
<td>0.32(0.06)</td>
<td>11</td>
<td>0.26(0.02)</td>
</tr>
<tr>
<td>Spruce Control</td>
<td>0.33(0.05)</td>
<td>0.34(0.03)</td>
<td>20</td>
<td>0.35(0.04)</td>
</tr>
<tr>
<td>Spruce Treatment</td>
<td>0.37(0.06)</td>
<td>0.31(0.04)</td>
<td>18</td>
<td>0.25(0.07)</td>
</tr>
</tbody>
</table>

1 Territory size of only those adults which were present during both the summer and autumn period.

2 All adults include squirrels present during both summer and autumn and adults which immigrated during autumn.
New animals and total animals captured

Before adding food, the number of new animals and total number of animals captured was similar between treatments (Table 3.3, Tukey HSD, $P > 0.09$ and $P > 0.06$, respectively) except for fewer total animals caught in Douglas fir control habitat. After supplemental food was added, I caught seven times as many new animals on the Douglas fir treatment grids as in Douglas fir control habitat ($P < 0.001$) and five times as many new animals in spruce treatment habitat as in spruce control habitat ($P < 0.003$). Similarly, I caught four times the total number of animals in Douglas fir treatment habitat as in Douglas fir control habitat and two times as many in spruce treatment habitat as in spruce control habitat. The number of new animals captured in Douglas fir and spruce control habitat did not differ ($P > 0.64$). Hence, the addition of supplemental food dramatically increased the number of new animals that remained on the grids long enough to be captured as well as the total number of animals captured.

The above results are supported by incidental observations on the behaviour of transient squirrels. While territorial residents were caught in traps, intruders often attempted to establish themselves on the "vacant" territories by feeding, exploring the central food middens and giving numerous advertisement calls. When released, residents always expelled the intruders, but this usually involved several extensive chases or fights over several hours. In one instance, three untagged intruders simultaneously attempted to claim the territory of a captured resident. Upon release, the resident could evict only two of the three intruders and subsequently lost part of its territory for 2 days before displacing the remaining intruder. Brief "territory take-overs" by intruders (while residents were caught in traps) were common on grids which received supplemental food, were seen once in spruce control habitat and were never observed in Douglas fir control habitat. In addition to attempting to establish territories more often during the absence of the owner, intruders also appeared to be more tenaceous in areas with supplemental food. New animals usually began to establish territories at a feeder or near the midden. When
Table 3.3. Mean numbers of previously untagged and total numbers (± 1 S.E.) of red squirrels captured during three live-trapping sessions in each season.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Untagged(^1)</td>
<td>Total</td>
</tr>
<tr>
<td>Fir Control</td>
<td>5.6 (0.75)</td>
<td>28.5 (3.00)</td>
</tr>
<tr>
<td>Fir Treatment</td>
<td>3.0 (0.75)</td>
<td>44.4 (6.10)</td>
</tr>
<tr>
<td>Spruce Control</td>
<td>5.4 (0.94)</td>
<td>50.5 (9.95)</td>
</tr>
<tr>
<td>Spruce Treatment</td>
<td>7.5 (1.50)</td>
<td>52.5 (1.49)</td>
</tr>
</tbody>
</table>

\(^1\) 1986 and 1987 data averaged, n = 2 for each treatment.
chased by the resident, they were very difficult to expel from the territory and would often return several times despite lengthy chases.

Changes in behaviour

To assess movement patterns, I calculated the mean distance moved per minute by animals which were active and when consecutive observations were less than 30 minutes apart. Squirrels moved over their territories at approximately the same rate in summer and autumn, regardless of the treatment (Table 3.4; $P > 0.53$). However, because territories were smaller in spruce habitat in summer (Table 3.1), squirrels in spruce habitat moved over their territories more "intensively" than animals in Douglas fir habitat. In autumn, the decrease in territory size of animals in Douglas fir habitat (especially those with supplemental food) resulted in a relative increase in the "intensity" with which squirrels moved over their territories.

Changes in the amount of time squirrels spent defending their territories with advertisement calls were estimated by recording the calls of focal animals (Table 3.5). Squirrels called at approximately the same frequency in all areas during both summer ($P > 0.44$) and autumn ($P > 0.37$). In autumn, squirrels called least often in Douglas fir control habitat but high variability masked any differences between treatments. If these data are viewed with respect to differences in territory size (Table 3.1), a different pattern emerges. During summer, squirrels called approximately twice as often in spruce control habitat as in Douglas fir control or Douglas fir treatment habitat. In autumn, squirrels in spruce control habitat and on areas with supplemental food called over four times as much per unit area of territory defended as animals in Douglas fir control habitat.

In summer, there was little difference in the mean proportion of time (estimated by the proportion of observations) that squirrels on each grid spent on feeding, food caching, resting and territorial behaviour between treatments ($P > 0.17$).
Table 3.4. Movement patterns of red squirrels in summer and autumn as estimated by distances moved (mean ± 1 S.E.). Values are expressed as meters per minute and represent the average of 1986 and 1987 data.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Summer 1 June - 10 Aug.</th>
<th>Autumn 20 Aug. - 10 Nov.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>m per min.¹</td>
<td>m per min.</td>
</tr>
<tr>
<td>Fir</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>16.8 (2.0)</td>
<td>17.4 (2.2)</td>
</tr>
<tr>
<td>Treatment</td>
<td>17.5 (0.6)</td>
<td>18.2 (0.1)</td>
</tr>
<tr>
<td>Spruce</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>17.6 (0.2)</td>
<td>18.4 (0.5)</td>
</tr>
<tr>
<td>Treatment</td>
<td>18.6 (2.1)</td>
<td>21.8 (3.4)</td>
</tr>
</tbody>
</table>

¹ n = 2 for each treatment. Distances calculated only during periods when animals were active.
Table 3.5. Mean numbers of territorial advertisement calls (± 1 S.E.) given by a focal animal per hour during behavioral monitoring in 1987.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Summer 1 June - 10 August</th>
<th>Autumn 20 August - 10 November</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td># of calls</td>
<td># of calls</td>
</tr>
<tr>
<td>Fir</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>2.03 (0.95)</td>
<td>4.60 (2.00)</td>
</tr>
<tr>
<td>Treatment</td>
<td>2.91 (1.33)</td>
<td>9.86 (2.88)</td>
</tr>
<tr>
<td>Spruce</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>5.83 (3.36)</td>
<td>9.44 (0.47)</td>
</tr>
<tr>
<td>Treatment</td>
<td>3.40 (1.07)</td>
<td>10.41 (0.43)</td>
</tr>
</tbody>
</table>

\(^1\text{n = 2 for each treatment.}\)
In autumn, feeding, food caching and resting behaviour were not different between treatments ($P > 0.29$), but the proportion of time spent on territorial defence behaviour increased on the food addition grids ($P < 0.019$). Squirrels in Douglas fir control habitat spent 13.9% of their time on defence compared to 16.6% in spruce control and 28.1% in both Douglas fir and spruce treatment habitat. Differences between the Douglas fir control and the food treatment areas were significant (Tukey HSD, $P < 0.032$) and marginally significant between the spruce control and treatment areas ($P < 0.081$).

When I added supplemental food, the increase in the proportion of time spent on territorial defence was related to both changes in numbers (Fig. 3.4a) and intruder pressure (Fig. 3.4b). Since population size and intruder pressure varied directly with food availability, I was not able to establish which of these two variables was responsible for the increase in defence behaviour.

I examined the effects of population size and the increased number of new animals captured on the proportion of time squirrels spent foraging away from their territory. I regressed the mean proportion of observations which were outside the territory boundaries against density in both summer and autumn (Fig. 3.5). In summer, the proportion of time spent away from the territory did not change with density ($r^2 < 0.01, P = 0.848$), while in autumn, it decreased with the increasing density of territorial residents ($r^2 = 0.35, P = 0.034$).

**DISCUSSION**

Territory size of red squirrels in Douglas Douglas fir habitat decreased when supplemental food was added but not in white spruce habitat. The results from Douglas fir habitat are consistent with the prediction of Patterson's (1980) resource-behaviour hypothesis that territory size fluctuates as food availability changes. In contrast, the
Figure 3.4. The relationship between the proportion of time spent on territorial defense vs. (a) density ($r^2 = 0.80, P < 0.003$) and, (b) intruder pressure ($r^2 = 0.75, P < 0.006$) in autumn. Density is the number of territories per 9 ha. and intruder pressure is the number of new (untagged) red squirrels captured during live-trapping while supplemental food was present. ○ and □ are fir and spruce controls, respectively, ● and ■ represent fir and spruce food addition treatments, respectively.
Figure 3.5. The proportion of time red squirrels spend away from their territory in (a) summer and in (b) autumn ($r^2 = 0.35, P = 0.034$). Dotted line in a indicates a non-significant trend. (Δ) indicates 1986 Douglas fir controls, (▲) 1986 Douglas fir treatments, (□) 1987 Douglas fir controls, (■) 1987 Douglas fir treatments, (◊) 1986 white spruce controls, (♦) 1986 white spruce treatments, (○) 1987 white spruce controls, (●) 1987 white spruce treatments.
inflexible territory size I observed in spruce habitat supports Southern's (1970) model of fixed territory size despite changes in food availability. I now discuss these results in light of differences in initial territory size in the two habitats and changes in behaviour which occurred as density increased.

\[ \text{Differences in territory and home range size} \]

Red squirrels in Douglas fir control habitat defended larger territories than squirrels in white spruce control habitat in both summer and autumn. Squirrel territories in spruce habitat were within the range reported from other studies (see Gurnell 1987 for a review) but the territories in Douglas fir habitat in summer (1.39 ha) were larger than those previously reported.

An absolute shortage of food was not evident in Douglas fir habitat. Large numbers of cones were produced annually and not harvested by squirrels or were clipped from branches but never cached in the midden. A similar pattern was noted in spruce habitat where there were often more than 100 cones per m\(^2\) on the ground under mature trees. Although both Douglas fir and spruce habitats had large numbers of uncached cones, the net effect may have been different in the two habitats. In the more mesic sites where spruce was common, the bracts of cones on the ground usually stayed closed throughout the day. In the drier Douglas fir habitat, cone bracts opened and closed as humidity changed during the day. During this process, seeds fall out and become available to other small mammals and birds. Hence, although the absolute levels of food produced in the two habitats may be similar, the cone mast in spruce habitat would remain available exclusively to red squirrels for longer periods.

Previous studies on use of space by red squirrels or the closely related Douglas squirrel (Rusch & Reeder 1978; Koford 1982; Gurnell 1984) have not differentiated between territories and home ranges. By using radio-telemetry and documenting the behaviours associated with each observation, I was able to distinguish territories from the
surrounding home ranges. Zach & Falls (1979) noted a similar pattern in ovenbirds: territories delineated by songs were exclusive and smaller than foraging areas which often overlapped the foraging areas of neighbors. I often observed squirrels that were away from their territories (and trespassing on another squirrel's territory) feeding on fungi which were often very abundant (up to 20 fungi per m$^2$) and remained available for 2 to 4 days before spoiling. When detected by the territory owner, trespassing squirrels avoided escalated conflicts by simply moving to different areas.

In my study, the home range area used by squirrels decreased from summer to autumn, but remained substantially larger than the territory. The reason for this decrease was not clear, although at the same time, food on the territory increased (cone mast ripened) and decreased outside the territory (fewer fungi in autumn). Also, there may be increased risks associated with foraging away from the territory in autumn. For example, the numerous dispersing juveniles may increase the need for residents to remain on and defend the territory (Krebs 1982). This would discourage intruders from attempting to settle and avoid the future costs of evicting such intruders when the resident returns. Foraging away from the territory may be a way to assess the status of surrounding territories (Bartels 1984, Finck 1984) or to explore and gain information on short or long term changes in resources (Gass & Montgomerie 1981; Tamm 1987; Shettleworth et al. 1988).

**Effect of supplemental food on territory size**

The addition of supplemental food decreased the territory size of red squirrels in Douglas fir habitat. Immigrants established territories within the area of former territories and in the interstices between territorial residents. In spruce habitat, most of the increase in the number of territories was the result of new territories being established in the interstices between territorial residents or in formerly vacant areas. These results differ from previous studies (Yom-Tov 1974; Hogstedt 1981) which indicated that
supplemental food does not result in new territories being established in formerly vacant areas. My results indicate that food can determine both territory size and what areas within a habitat are defended.

I could not separate the effects of increased food and intruder pressure on territory size directly, but several observations suggest that intruder pressure had a stronger influence. When supplemental food was first added, the owners of large territories began to feed on the sunflower seed within several days but did not contract their territory boundaries. Intruders established small territories (often at a feeder station) near the periphery of an existing territory and then expanded. Territorial residents contracted their boundaries only after extended interactions (up to three hours of advertisement calls, chases and occasional fights) with these newly established intruders. These observations are consistent with the view that intruder pressure is the primary factor that influences territory size (Myers, Connors, & Pitelka 1979, 1981; Norton, Arcese, & Ewald 1982, but see Boutin & Schweiger 1988). However, food availability and intruder pressure are closely interrelated since high intruder pressure was observed only on the areas where I increased food abundance in relation to the surroundings (Hixon 1980).

My results from spruce habitat support Southern's (1970) hypothesis and Rusch & Reeder's (1978) conclusion that territory size of red squirrels does not change despite fluctuations in food availability. In studies of territory size of reef fish, Norman and Jones (1984) and Tricas (1989) also found that changing food abundance had little effect on territory size. However, at high levels of supplemental food, Tricas (1989) noted that territory size decreased after intruder pressure increased. Home range size in lizards did not decrease when supplemental food was added (Waldschmidt 1983; Jones, Waldschmidt & Potvin 1987; Guyer 1988) and Fransblau & Collins (1984) reported no change in territory size when mealworms were provided to an insectivorous bird.

By maintaining a constant territory size while food resources fluctuate, an individual may enhance its chances of surviving or reproducing during subsequent
periods of food shortage (Seastedt & MacLean 1979; Lima 1984; Houston, McCleery & Davies 1985). Territories larger than necessary for current food requirements may be defended as insurance against food robbing by neighbors, unpredictable weather or lowered foraging efficiency resulting from resource depression (Charnov, Orians & Hyatt 1976; Salomonson & Balda 1977; Ewald & Carpenter 1978) and may help avoid the costs of evicting conspecifics as food resources decrease (Ewald and Carpenter 1978; Myers, Connors & Pitelka, 1981; Von Schantz 1984a). The changing territory size I observed in Douglas fir habitat and inflexible territory size in spruce habitat indicates the response to changing food availability varies with population density or environmental conditions. These data support the "elastic disk" model of territory size proposed by Huxley (1934). Although territory size may initially be flexible, there is increased resistance to further compression as territory size continues to decrease.

Red squirrels may use several cues to establish and defend territories of fixed size. Habitat characteristics (Stenger 1958; Newton et al. 1977; Seastedt & MacLean 1979) may be important, especially if animals establish residence during years of abundant food. Also, the presence of conspecifics (Stamps 1987, 1988) or traditional cues (Shields et al. 1988) can help an animal decide where to establish residence. Red squirrels' central middens may dependably indicate long-term territory quality; intruders usually investigate middens before they attempt to settle and begin to defend territories. Although middens may provide a cue about habitat quality, it appears that current food abundance can override this information. On the food addition areas, new residents resurrected old middens which had not been used for several years or began to establish new middens.

Changes in behaviour

Red squirrel territories in Douglas fir treatment habitat decreased to the size of territories in spruce habitat but in both areas, excess food remained in feeders or cached
in midden. I provided supplemental food in a regular pattern (9 food stations per ha) so
that individuals could not monopolize and restrict the access of intruders to a single large
feeder (Ewald and Carpenter 1978; Monaghan & Metcalfe 1985). However, squirrels
could still defend a large area which contained more than two feeders on even the
smallest territories. Potential immigrants were present throughout the period of
supplemental food but after an initial increase in density during the first 4 - 6 weeks
(Chapter 2), few new animals established themselves.

As the number of territories on the treatment areas increased, the proportion of
time spent on territorial defence also increased. This change may have been a response
to the increase in intruder pressure or an increase in the amount of time available for
territorial defence (Ydenberg 1984) since sunflower seeds were more easily obtained and
utilized than cones. If increased food resources are detected by other animals and this
leads to changes in intruder pressure (Ewald & Carpenter 1978; Hixon 1980; Myers,
Connors & Pitelka 1981), an individual defending an enriched territory of fixed size
would need to increase territory defence to deter competitors. Animals can increase
territory defence by accepting satellites (Davies and Houston 1981) or increasing the
proportion of time spent on defence (Tricas 1989).

The effect of increasing the proportion of time spent on territorial defence would
be enhanced by the unchanging movements and constant level of advertisement calls on
the food addition areas. By maintaining a constant rate of travel, squirrels on smaller
territories would be traversing or patrolling their territories more often and this may
enable them to detect intruders sooner. I suggest that these changes in behaviour and the
decline in the proportion of time spent foraging outside the territorial boundaries may
enable red squirrels to resist a further decrease in territory size despite continued high
intruder pressure.

Few studies have reported behavioural responses to changing food availability.
Responses to increased food include: (1) increased aggressiveness or increased intensity
of territorial defence (Ydenberg 1984; Ims 1987), (2) increased use and defence of the
territory (Ewald & Carpenter 1978; Ewald & Bransfield 1987; Tricas 1989), (3) no
change in territory defence (Hixon, Carpenter & Paton 1983; Gass & Sutherland 1985),
(4) a decrease in the proportion of time spent on foraging and feeding (Hixon, Carpenter
& Paton 1983; Gass & Sutherland 1985) and, (5) the acceptance of satellites on the
territory to help with defence (Davies & Houston 1981). Stamps & Tanaka (1981)
oberved an increase in display rate and a decrease in home range size of lizards in the
short term but these effects were not significant after several days. Several studies have
reported that behaviour did not change when supplemental food was added (lizards:
birds: Enoksson 1988), but it is not clear in some cases whether food was a limiting
resource during the period of study (Norman & Jones 1984; Jones, Waldschmidt &
Potvin 1987).

**Territorial behaviour, food resources and population dynamics**

When I supplied sunflower seed to red squirrels, new territories were established
between existing territories and in Douglas fir habitat, large territories decreased in size.
However, as density increased, red squirrels spent more time defending their territories,
enabling them to defend territories larger than necessary for current food requirements.
This suggests a complex relationship between resources, behaviour and population
response. At low density (i.e. in Douglas fir habitat), increased food abundance results in
an increase in population density as territories decrease in size. At high density, such as
in white spruce habitat or when population density reaches its maximum in Douglas fir
habitat, behavioural changes compensate for the increase in per capita resources and little
change in density occurs. Current food availability no longer appears to be a limiting
factor, and territories are being defended on the basis of a different limiting resource or
the prospective value of food resources on the territory (Stamps & Tollestrup 1984).
Hence, before drawing conclusions about the factors which affect spacing behaviour and population density, experiments should be conducted in a range of habitats and population densities.

Changes in territory size and defence behaviour will depend on the type of foods utilized (are they defendable and can they be stored?), their availability through time (variable or continuous), and how long an individual lives on the territory (Stamps & Tollestrup 1984, Von Schantz 1984a). For example, migratory hummingbirds adjust territory size on a daily basis to changes in food availability (Hixon, Carpenter & Paton 1983). However, unlike breeding residents, migratory animals do not need to evict neighbors when resource levels decrease: they simply move on to other foraging areas. In contrast, non-migratory animals such as the red squirrel could offset fluctuations in resources by defending territories which contain more food than currently required and caching surplus food. The ability to cache surplus food can alter the relationship between territory costs and benefits. Instead of reaching maximum benefits at current food requirements, maximum benefits may occur at a larger territory size or continue to increase, depending on the type of food being cached.

From the limited information available on changes in behaviour during fluctuations in food abundance, several patterns can be derived (Fig. 3.6). I predict that animals which live for a long time in relation to resource fluctuations or that use foods which are defendable or can be stored, will respond to changes in food abundance and changes in competitor density by increasing the level of territorial defence. Such changes in territorial defence behaviour may explain the "increased resistance to further compression" which underlies the elastic disk model of territory size proposed by Huxley (1934). Migratory animals or individuals which hold territories for only a short time and those which cannot store food should defend flexible territories, and as a consequence, density will fluctuate.
Figure 3.6. A conceptual model outlining the relationship between changes in food abundance, changes in territory defense behaviour and population stability.
The changes in red squirrel territory size and behaviour which I observed after adding supplemental food may be representative of small mammals which feed on a defendable resource such as seed. This response can explain the 2-3 fold increase in population density which Gilbert and Krebs (1981) suggested was normal for food addition studies of small mammal populations. However, similar results have been reported for microtine and lagomorph populations which may not be territorial and I suggest that other mechanisms are responsible for the limited response in these species.

The results of the present study should be viewed in light of the constraints imposed by the experiment itself. Although I tried to simulate a natural increase in food abundance, the manipulation remains artificial. The lack of a decrease in territory size in spruce habitat can thus be interpreted in two ways: (1) this is the lower limit of territory size for red squirrels, or (2) the particular type or dispersion of food was not adequate to effect a greater response. Such shortcomings are common to most ecological experiments (Price 1986; Wiens, Rotenberry & Van Horne 1986) and can only be resolved by further studies. Experiments which manipulate food (at several levels and patterns of dispersion) and simultaneously monitor changes in behaviour would address these questions.
Chapter 4

SETTLEMENT PATTERNS AND RESPONSES TO REMOVALS

INTRODUCTION

Watson & Moss (1970) argued that to demonstrate that territorial behaviour limits breeding population density, there must be a surplus of animals and these animals must breed if given the opportunity. Spacing behaviour can also limit juvenile recruitment in autumn by forcing animals to disperse or by preventing conspecifics from settling (Watson & Jenkins 1968; Slade & Balph 1974; Thompson 1978; Smith 1980; Brody & Armitage 1985; Hanson & Nixon 1985; Danielson & Gaines 1987). There is considerable evidence that spacing behaviour can limit breeding density in both birds (Krebs 1971; Zwickle 1980; Hannon 1983; Gauthier & Smith 1987) and small mammals (Krebs, Redfield & Taitt 1978; Henderson 1979; Boonstra & Rodd 1983; Taitt 1985a). By limiting breeding density or recruitment, territorial behaviour may affect the overall population density if the animals which are not successful in obtaining a territory have lower survival than residents (Jenkins, Watson & Miller 1963; Watson 1985) and food or other resources are not limiting.

If population density is limited by territorial behaviour, then the factors which affect territory size will also influence population density (Hixon, Carpenter & Paton 1983). Settlement patterns have been shown to affect territory size (Van den Assem 1967; Zahavi 1971), and hence, episodes of high mortality (e.g. during harsh winters or intense predation) may create the conditions to increase density when the population recovers. Although theoretical considerations have demonstrated that simultaneous settlement should increase density (Maynard Smith 1974; Tanemura & Hasegawa 1980), field studies on the effect of simultaneous settlement have been equivocal (Knapton & Krebs 1974; Taitt 1985b).
To determine whether territorial behaviour limits breeding density and juvenile recruitment of red squirrels at both high and low population density, I conducted a series of pulsed removal experiments in good (high squirrel density, white spruce) and poor (low squirrel density, Douglas fir) habitat. I used asynchronous and simultaneous removals to assess the importance of settlement patterns on the subsequent density of red squirrels. I predicted that if territorial behaviour limits breeding density, then the animals I removed in spring would be replaced by animals capable of breeding. Since males are promiscuous during the breeding season (C. Smith 1968), I considered the availability of females to be the main factor limiting breeding density (Hannon 1983). I also predicted that if the territorial behaviour of residents limits recruitment in autumn, squirrels which are removed at that time should be replaced by immigrants. Furthermore, I predicted that if settlement patterns affect territory size, simultaneous removals should result in decreased territory size and increased recolonization density compared with the density on control or asynchronous removal areas.

In the final year of the study, I conducted a simultaneous removal and concurrent food addition experiment to evaluate the role of resident squirrels on the population response to increased food abundance. I predicted that if simultaneous settlement had a strong influence on territory size, recolonization density would be greater on the areas where residents had been removed prior to adding supplemental food than where residents were left in place. By removing residents (without concurrent introductions), I attempted to establish the appropriate conditions for simultaneous settlement and relied on immigrants to colonize the removal areas.

METHODS

The study area was located in south-central British Columbia, Canada, near the village of 100 Mile House (51° 42' N; 101° 24' W). A summary of vegetation characteristics of
the area, red squirrel population estimates, behavioural monitoring and the supplemental food used has been described previously (Chapter 2).

*Removal experiments*

In Douglas fir habitat, two removal grids were monitored from 1985-88. In spruce habitat, there was one removal area in 1986 and two removal areas from 1987-88. In spruce habitat, one removal grid was rectangular (8x11, 7.9 ha.) and the second had a large open sedge meadow which reduced the area of suitable habitat to 8.4 ha. Control areas for the removal populations have been described in Chapter 2.

Red squirrels were removed from the trapping grids in either of two patterns (Table 4.1). Simultaneous removals were conducted during the two day live-trapping session. Asynchronous removals were carried out over a three week period using the following procedure. I first determined the center of activity of all animals which were residents on the trapping area by plotting the locations where an animal had been live-trapped or where animals with coloured ear tags were seen. Observations of animals giving territory advertisement calls near the large central cache of stored cones were considered to be good estimates of the territory activity center. After determining the approximate center of activity, I selected two or three animals for removal each week such that there was always one or two occupied territories between the animals being removed. This procedure was continued until all residents had been removed.

All animals captured were removed from the study area and released between 5 and 10 km from the point of capture. Of the 267 animals removed from the trapping grids, only two squirrels returned to the area from which they had been removed (5.3 and 8.1 km) and only one of these animals reestablished itself on its previous territory.

During the removal experiments, I attempted to remove all animals resident on the study areas. This included squirrels on the immediate periphery of the 9 ha study plots and hence increased the effective removal area by approximately 30%. I verified
Table 4.1. Date and type of removal conducted in Douglas fir and white spruce habitat from 1985 to 1988. The number of male and female red squirrels removed is indicated in parentheses.

<table>
<thead>
<tr>
<th></th>
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<th></th>
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<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Douglas Fir #1</strong></td>
<td><strong>21 April-5 May</strong></td>
<td><strong>6-7 April</strong></td>
<td><strong>14-15 April</strong></td>
<td></td>
</tr>
<tr>
<td></td>
<td>A (2,3)</td>
<td>S (2,2)</td>
<td>S (9,4)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>28-29 August S (0,4)</td>
<td>24 Sept.-10 Oct. A (6,9)</td>
<td>24 - 25 August S (2,3)</td>
<td>22-23 August S+F (7,13)</td>
</tr>
<tr>
<td><strong>Douglas Fir #2</strong></td>
<td><strong>23-24 April</strong></td>
<td><strong>6 - 7 April</strong></td>
<td><strong>13-14 April</strong></td>
<td></td>
</tr>
<tr>
<td></td>
<td>S (4,6)</td>
<td>S (4,2)</td>
<td>S (3,5)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3 Sept.-6 Dec. C (21,20)</td>
<td>24-25 Sept. S (9,8)</td>
<td>24-25 August S (0,0)</td>
<td>22-23 August S (7,4)</td>
</tr>
<tr>
<td><strong>Spruce #1</strong></td>
<td><strong>26-28 May</strong></td>
<td><strong>8-9 April</strong></td>
<td><strong>15-16 April</strong></td>
<td></td>
</tr>
<tr>
<td></td>
<td>S (20,14)</td>
<td>S (2,6)</td>
<td>S (5,5)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>23-24 Sept. S (11,4)</td>
<td>13 Aug.-16 Sept. A (5,3)</td>
<td>24-25 August S+F (6,2)</td>
<td></td>
</tr>
<tr>
<td><strong>Spruce #2</strong></td>
<td><strong>16-17 April</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>S (3,3)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>6-7 September S (3,3)</td>
<td>24-25 August S (4,9)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1 Indicates the type of removal. A = asynchronous, S = simultaneous, C = continuous, S+F = simultaneous removal and concurrent food addition. See text for a description of methods.
the residency status of animals by two methods. First, from trapping records, I estimated which animals were resident on the grid by how consistently they were captured during previous trapping periods and by the spatial stability of capture locations between trapping periods. In a previous study (Chapter 3), this approach gave close agreement with residency status as determined from intensive behavioural monitoring of animals equipped with radio-telemetry collars. Secondly, I conducted systematic searches for animals with coloured ear tags and noted the location of the center of activity of specific animals. The residency status of animals based on trapping data closely agreed with the information on residency based on visual observations and telemetry monitoring on the Douglas fir removal area in 1988.

**Simultaneous removal with supplemental food**

Supplemental food (sunflower seed) was added to one grid in each habitat in 1988 immediately after the simultaneous removal of all animals. This experiment ensured that intruder pressure was high, and that newcomers and recruits would attempt to settle in the area. In Douglas fir habitat, *ad libitum* supplemental food was added from 25 August to 24 October. Due to cost and logistic constraints, I was only able to add food to an 8 ha area on this grid. In spruce habitat, supplemental food was added as a single pulse on 25 August. After the sunflower seed had been present on this area for about a week, black bears (*Ursus americanus* Pallas) began to forage in the area and damage feeders, forcing me to discontinue feeding. Hence, supplemental food was only available in this area for 2-3 weeks.

**Territory size**

I monitored the territory size of red squirrels in Douglas fir habitat from 10-25 August 1988 on an area where all animals had been removed simultaneously earlier in spring (14-15 April). I compared these data on territory size from the simultaneous
removal area with estimates of territory size on a control area in Douglas fir habitat which was monitored from 15 August to 20 September in 1987 when population density in the two areas was similar.

**Analyses**

Since I did not observe differences in population density in response to simultaneous vs. asynchronous removals, I used data from the two patterns of removals as replicates. The mean number of newcomers and recruits was the number of animals of each type captured during four live-trapping sessions after a removal trial and averaged over the number of removals conducted between 1985 and 1988. I compared treatment effects with a one-way ANOVA and the Tukey HSD multiple comparisons test.

To decide if simultaneous settlement enhances density, I used the 1.7-fold increase in density reported by Tanemura & Hasegawa (1980) as a guide to a significant effect. Because control population density fluctuated or was consistently higher than the density on the removal areas, I compared population responses on the removal area to both control population density and pre-removal density on the removal areas.

**RESULTS**

*Population density*

Red squirrels in both the control and removal areas had similar trappabilities. The overall Jolly trappability in Douglas fir habitat ranged from an average of 69% (control) to 74% (removals). In white spruce habitat, trappability averaged 82% on the control areas and 71% on the removals.

In Douglas fir habitat, population density recovered to control or pre-removal density in four of six trials when red squirrels were removed in autumn (Fig. 4.1). After removal, there was usually a rapid increase in density to control levels through
Figure 4.1. Changes in density following the removal of resident squirrels in Douglas fir habitat, 1985 to 1988. (a) Douglas fir removal area #1, (b) Douglas fir removal area #2. Shading represents the timing of removal episodes; (S) indicates a simultaneous removal, (A) indicates an asynchronous removal. See text for a description of removal methods. (○) and (□) represent control populations, (●) and (■) represent removal treatments. Density (MNA) calculated as the number of red squirrels per 9 ha.
immigration. In 1986, population density on neither removal area (simultaneous or asynchronous) increased to control or pre-removal density. As indicated by the continued immigration of newcomers during the five consecutive removals in Douglas fir habitat (3 September to 9 December 1985, Fig. 4.1b), there was a sufficient number of immigrants available to colonize removal areas until at least mid-December. When residents were removed in spring, density recovered to control or pre-removal levels in five of six trials. In 1987, adults did not immigrate onto one of the removal areas (Fig. 4.1b) and density did not increase until juveniles began to colonize the area in July.

In spruce habitat, population density returned to control or pre-removal densities in three of four removal trials in spring and three of four removal trials in autumn (Fig. 4.2). As in the removal experiment in Douglas fir habitat, population density did not recover to pre-removal or control densities after the autumn removal in 1986. In the spring of 1988, density remained low after residents had been removed (Fig. 4.2a). However, density on this grid had been declining since early winter and it is not clear whether resources were declining or there were too few animals available to fill vacant territories. The second removal area in spruce habitat (Fig. 4.2b) had a lower overall density compared to the two control areas or the other spruce removal area.

The pattern by which resident squirrels were removed (simultaneous or asynchronous) did not affect the subsequent recolonization density in either Douglas fir or spruce habitat. After residents were removed, immigrants either re-established the pre-removal density or returned to the population density on the control areas (Figs. 4.1, 4.2).

Recruitment

Population density on the removal areas returned quickly to control levels through the immigration of newcomers, some of which became recruits. In spring, there were
Figure 4.2. Changes in density following the removal of resident squirrels in white spruce habitat, 1986 to 1988. (a) White spruce removal area #1, (b) white spruce removal area #2. Shading represents the timing of removal episodes; (S) indicates a simultaneous removal, (A) indicates an asynchronous removal. See text for a description of removal methods. (○) and (□) represent control populations, (●) and (■) represent removal treatments. Density (MNA) calculated as the number of red squirrels per 9 ha.
Table 4.2. The mean number (± 1 S.E.) of newcomers and recruits captured during four live-trapping sessions after removals in spring and autumn. Data averaged over the removals conducted between 1986 and 1988.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Spring Newcomers</th>
<th>Spring Recruits</th>
<th>Autumn Newcomers</th>
<th>Autumn Recruits</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fir Control</td>
<td>9.0 (1.7)</td>
<td>3.7 (0.4)</td>
<td>12.7 (1.7)</td>
<td>4.6 (0.1)</td>
</tr>
<tr>
<td>Fir Removal</td>
<td>20.2 (1.2)</td>
<td>6.7 (1.7)</td>
<td>12.5 (0.6)</td>
<td>6.9 (1.6)</td>
</tr>
<tr>
<td>Spruce Control</td>
<td>13.5 (3.5)</td>
<td>1.7 (1.7)</td>
<td>8.8 (2.8)</td>
<td>5.4 (1.1)</td>
</tr>
<tr>
<td>Spruce Removal</td>
<td>18.7 (3.7)</td>
<td>8.5 (1.5)</td>
<td>26.3 (6.8)</td>
<td>9.0 (2.0)</td>
</tr>
</tbody>
</table>
more newcomers and recruits on the removal areas within each type of habitat than on the control areas (Table 4.2). These differences were not significant \((P > 0.118\) and \(P > 0.164\) for newcomers and recruits, respectively) but indicated a trend towards more animals attempting to, and being able to settle on the removal areas. In autumn, the pattern of recruitment was similar to that in spring (Table 4.2). The same number of newcomers were caught on the Douglas fir control and Douglas fir removal areas but more of these were able to establish themselves as recruits on the removal areas than on the control areas. In spruce habitat, more newcomers were captured on the removal areas than on the controls. As in spring, consistently more recruits were caught on the removal areas than on the control areas but the difference was not significant \((P > 0.089\) and \(P > 0.240\) for newcomers and recruits, respectively).

**Breeding**

In Douglas fir habitat, females which established themselves on the removal areas came into breeding condition in all years except 1987 (Table 4.3). In 1988, females did not reach breeding condition until mid-July on the second removal area in Douglas fir habitat. The proportion of breeding females on the removal areas was lower than in control habitat where virtually all females came into breeding condition (Chapter 2).

In spruce habitat, females capable of breeding immigrated to one of the removal areas after each removal in spring. On the second spruce removal area, (only one spring removal in 1988), I did not capture females in breeding condition until mid-July, suggesting there were few surplus females willing to immigrate into this area earlier in the year.
Table 4.3. Presence of breeding females\(^1\) and proportion of females captured which were in breeding condition after removals in spring.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>1986</th>
<th>1987</th>
<th>1988</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fir Removal #1</td>
<td>Yes (2/5)(^2)</td>
<td>Yes (5/6)</td>
<td>Yes(^3) (4/5)</td>
</tr>
<tr>
<td>Fir Removal #2</td>
<td>Yes (4/8)</td>
<td>No (0/0)</td>
<td>Yes (3/6)</td>
</tr>
<tr>
<td>Spruce Removal #1</td>
<td>Yes (3/5)</td>
<td>Yes (6/6)</td>
<td>Yes (5/6)</td>
</tr>
<tr>
<td>Spruce Removal #2</td>
<td>-</td>
<td>-</td>
<td>Yes(^3) (3/5)</td>
</tr>
</tbody>
</table>

\(^1\) Females in breeding condition were present on all control areas during the 1986 to 1988 period. Males in breeding condition were captured on all grids after each removal experiment in spring.

\(^2\) Indicates the number of females in breeding condition and the total number of females captured.

\(^3\) Females in breeding condition not present until mid-July.
Territory size

The territory size of red squirrels in Douglas fir habitat did not decrease after the simultaneous removal of adults in the spring of 1988 (Fig. 4.3). The average territory size of squirrels on the removal grid (0.70 ha) was similar to the territory size of squirrels on the control area in the autumn of 1987 (0.64 ha) when density on the two areas was approximately the same.

Supplemental food and removals

When supplemental food was added to the simultaneous removal areas, there was a marked increase in density through immigration (Fig. 4.4). In Douglas fir habitat, density increased to forty animals per 9 ha and in spruce habitat, to twenty-five animals per 9 ha. When supplemental food was added, there was a marked increase in both the number of newcomers and recruits. In Douglas fir habitat, I captured three times as many newcomers (thirty-eight vs. thirteen) and five times as many recruits (twenty-six vs. five) on the simultaneous removal area which received supplemental food as on the other simultaneous removal area. In spruce habitat, I captured thirty newcomers and twenty recruits where supplemental food was added, compared to eighteen newcomers and five recruits on the simultaneous removal area without supplemental food.

DISCUSSION

Effect of territorial behaviour on population density

My removal experiments indicated that territorial behaviour limited both breeding density in spring and the recruitment of immigrants in autumn. Breeding density and recruitment were limited by territorial behaviour both in Douglas fir and white spruce habitat, but at a lower density in Douglas fir habitat. Female immigrants bred in both
Figure 4.3. 90% convex polygon estimates of red squirrel territories in Douglas fir habitat. (a) Territories monitored in control habitat during autumn, 1987 (15 August to 20 September). (b) Territories on a removal area in Douglas fir in autumn, 1988 (15 August to 25 August) after the simultaneous removal of residents in spring. Each polygon represents a different animal.
Figure 4.4. Change in population density in 1988 after the simultaneous removal of animals in spring (S) and the simultaneous removal and addition of food in autumn (S+F). (a) Douglas fir habitat, (b) white spruce habitat. Shaded bars indicate the timing of removals. (ocio) indicates the control population, (■) is the simultaneous removal only and (●) is the simultaneous removal plus supplemental food. Density calculated as the number of red squirrels per 9 ha.
habitats, thus satisfying the first two of Watson & Moss's (1970) criteria to show that breeding density is limited by spacing behaviour. The presence of residents may discourage potential immigrants from settling through an assessment of per capita resource availability or through interactions with residents (interference competition). For example, if an animal is already present in the area, a potential immigrant may decide to search for another area with higher food availability rather than stay. Direct observations on red squirrels on the control and removal areas indicated that red squirrels expelled intruders and that settlement on the territories of residents was prevented by direct interference. The unequal immigration of red squirrels to fill territory vacancies in Douglas fir and spruce habitat, combined with observations of direct interference, is consistent with the "ideal despotic" model of habitat selection (Fretwell & Lucas 1970). This model predicts that animals should attempt to defend territories in good habitat before filling vacancies in lower quality areas.

Although population density on the study grids was limited by territorial behaviour, the implications of territorial behaviour for overall density are not clear. Squirrels which immigrated to the removal areas were usually of unknown origin and the fate of these animals had they not obtained a territory is not known. These animals may suffer high mortality (Watson 1985) or they may be able to exist as "floaters" (S. Smith 1978) until a vacancy occurs. Krebs (1971) was able to demonstrate that birds which filled vacancies in prime habitat came from hedgerow areas where they had lower breeding success. C. Smith (1968), Kemp & Keith (1970) and Rusch & Reeder (1978) stressed that red squirrels need territories to enable animals to establish winter food caches. They suggest that squirrels which cannot obtain territories and those with poor territories suffer high overwinter mortality. If this is true for red squirrels in my study, territorial behaviour would also limit overall population density but as noted by Smith, Arcese & Hochachka (in press), the fate of all animals in the population should be known.
Sinclair (1986, 1989) has questioned the applicability of the Watson and Moss (1970) criteria, pointing out that the survival of animals which were not able to obtain a territory is assumed to be lower than if territorial behaviour had not existed. However, this may not always be the case. For example, if territory size fluctuates with resource abundance, then territorial behaviour may simply determine which animals get to recruit or breed. There is some indication that territorial behaviour of red squirrels (and possibly other animals which defend "long-term" territories (Patterson 1980) may limit overall population density. When I added excess supplemental food, territory size of squirrels in white spruce habitat did not decrease (Chapter 3), suggesting that more animals would have been able to survive on these areas if territorial behaviour had not been present.

When adults were removed from white spruce habitat in spring, territorial vacancies were usually filled by immigrants capable of breeding. In contrast, territory vacancies were not always replaced in Douglas fir habitat as indicated by the lack of immigrants after spring removals in 1987. The difference in immigration between Douglas fir and spruce habitat after spring removals may reflect differences in habitat quality (Chapter 2) combined with a limited number of animals searching for vacant territories. Hence, territorial behaviour may not limit breeding density in poor habitat in all years and territorial behaviour at these times may simply space individuals out within the available habitat (Lack 1954). Thus, before drawing general conclusions about the effect of territorial behaviour on population density, it is important to study populations in a range of habitats and over a period several years.

Settlement patterns

In evaluating the effect of settlement patterns on territory size and population density, Tanemura & Hasegawa (1980) suggested that simultaneous settlement should lead to approximately a 1.7-fold increase in density. Evidence from studies of captive animals in artificial environments (Van den Assem 1967; Zahavi 1971) and some field
studies appear to support theoretical predictions. Tompa (1964) observed an increase in
the breeding density of song sparrows (Melospiza melodia) on an island after an episode
of high mortality in spring. Similarly, Knapton and Krebs (1974) indicated that territory
size and density of a population of song sparrows increased after simultaneous removals
in autumn, but in their study, density declined before the next breeding season. However,
when Watson and Jenkins (1968) removed territorial male red grouse (Lagopus lagopus
scoticus), recolonization densities were not consistently higher than the initial density.
Taitt (1985b) introduced voles (Microtus townsendii) onto removal areas but did not
observe an increase in density where voles were introduced simultaneously.

The simultaneous and asynchronous removals I conducted on red squirrels did not
lead to a decrease in territory size or an increase in recolonization density on the
simultaneous removal areas. Although consistent across several trials, these results are
not conclusive since the experiments were not replicated in each habitat. Several factors
may have contributed to the lack of a response. In autumn, there may have been too few
animals available to colonize the removal areas, but evidence from the food addition
experiment suggests that numerous newcomers were available. Price et al. (1986) also
found that territory size did not decrease when either single red squirrels or groups of
four animals were removed. One assumption of the simultaneous settlement model used
by Tanemura & Hasegawa (1980) is that the habitat must be homogeneous. On the scale
of the experiments I conducted, this assumption was not met and subtle habitat features
may have provided cues regarding the placement of territory boundaries. It is not clear
what cues are used by red squirrels when establishing their territories, but one prominent
feature which may reflect habitat quality is the central midden in which animals cache
cones. Middens remain visible for several years and may provide cues about long term
habitat quality when food abundance cannot be directly assessed (Shields et al. 1988).
Hence, although simultaneous removals may eliminate residents which could be used as
foci about which to establish territories (Stamps 1987, 1988), artifacts which reflect previous density remain.

Simultaneous settlement and food

To examine the relative influence of settlement patterns and food availability on recolonization density, I conducted a simultaneous removal and provided *ad libitum* sunflower seed immediately after the removals. Simultaneous settlement did not increase population density compared to the areas where food was added but residents left in place (Chapter 2). Supplemental food did increase density and recruitment through immigration, indicating that a pool of newcomers was available in the population. Taitt (1985b) noted a similar pattern for *Microtus townsendii*.

When supplemental food was added to the simultaneous removal area in Douglas fir habitat, the removals may not have enhanced the increase in density because the conditions for simultaneous settlement were not met. During a systematic search of the area three days after supplemental food was added, I noticed that only a few animals had immigrated onto the grid. Hence, although I had created the appropriate conditions for simultaneous settlement, there may not have been a sufficient number of juvenile immigrants available to colonize the area in one pulse. A more appropriate experiment would have been to add supplemental food and wait for several weeks before removing all residents. This design would ensure that surrounding animals would be familiar with the increased food resources and that the conditions necessary for simultaneous settlement would be met.
Chapter 5

GENERAL CONCLUSIONS

This thesis makes contributions in four areas of population ecology. (1) In Chapter 2, I demonstrate that red squirrel populations are limited by food in both poor and good quality habitat (low and high squirrel density) and show that the difference in density between these two habitats is due to food availability. I demonstrate that recruitment is density-dependent in the presence of excess food and that the population decline after supplemental feeding ended is also density-dependent. (2) In Chapter 3, I show that the relationship between food abundance and territory size in red squirrels is complex, and that the effect of food on territory size is influenced by competitor density. (3) I present evidence in Chapter 4 which suggests that both breeding density and juvenile recruitment is limited by the territorial behaviour of residents. (4) In Chapter 4, I also show that settlement patterns have little influence on the territory size or density of recolonizing animals.

Food limitation of red squirrels

The hypothesis that food abundance limits populations of small mammals has received considerable support from a growing number of food addition experiments (Boutin 1990). Rusch & Reeder (1978) hypothesized that red squirrel populations were regulated by territorial behaviour about a level set by food abundance in years of poor cone crops. A number of studies on small mammals have indicated that spacing behaviour and competition for space appears to regulate populations, but the role of food in this relationship is not clear (Sinclair 1989). My results show that food limited both low and high density populations of red squirrels, but density-dependent recruitment in the presence of excess food indicated that another factor regulated the population.
Changes in territory size

In a review of food addition studies, Gilbert & Krebs (1981) noted that most small mammal populations show a 2-3 fold increase in density when excess supplemental food is added, and suggested that research should focus on why the response is not greater. Boutin (1990) outlined four possible explanations for this general pattern: (1) another resource becomes limiting after density doubles, (2) food again becomes limiting because of the way it was distributed, (3) the census area increased when food is added (i.e. an aggregation response) and, (4) food was not provided long enough to generate a larger response.

The ad libitum food addition I discuss in Chapter 2 resulted in a 2-4 fold increase in red squirrel density. By monitoring behaviour directly, I was able to show that food was always in excess (more than two feeders per territory) and that there was a real increase in density (the number of territories increased). The rapid increase in the number of territories and the density dependent recruitment rate suggest that the length of time that food was available was not a factor in limiting the response and that another factor is preventing a further increase.

The increase in the proportion of time spent on territorial defence provides a mechanism to resist a further decrease in territory size and supports the "elastic disk" model of territory size proposed by Huxley (1934). I originally set out to test whether the inflexible territory size hypothesis (Southern 1970; Rusch & Reeder 1978) or the resource-behaviour hypothesis (Patterson 1980) applied to red squirrels. My results show that population and behavioural responses to changing food abundance are complex. At low population density (large territory size), territory size decreases and these results support the resource-behaviour hypothesis. At high population density (small territory size), territory size did not decrease and these findings support the inflexible territory size hypothesis. By increasing the amount of time spent on territorial defence, squirrels were able to defend territories larger than necessary for current food requirements. Based on
these results, I present a conceptual model (Chapter 3) which outlines the relationship between changing food resources, territorial defence behaviour and population stability.

**Territorial behaviour, breeding density and juvenile recruitment**

Removal experiments in spring and autumn and the subsequent recolonization of these areas indicated that the presence of residents can limit both breeding density and juvenile recruitment. These results support the hypothesis that territorial behaviour can limit population density (Brown 1969; Watson & Moss 1970) but several unknowns remain. I was not able to document the fate of squirrels who did not establish territories, hence the effect of territorial behaviour on overall population density is not clear (Smith & Arcese 1986; Smith, Arcese & Hochachka *in press*). Further studies which are able to follow all animals in the population are needed.

**Settlement patterns**

Simultaneous settlement can reduce territory size and lead to an increase in population density (Van den Assem 1967; Maynard Smith 1974; Tanemura & Hasegawa 1980). The events which lead to a decrease in territory size are not well understood, but the lack of residents about which to establish territories (Stamps 1987, 1988) and a change in the pattern of aggression by the new residents (Patterson 1980) have been suggested. My results indicate that simultaneous settlement does not influence territory size or increase recolonization density of red squirrels. Other studies (Watson & Jenkins 1968; Taitt 1985b) have reported similar results; but a number of questions remain. Although I attempted to provide the appropriate conditions for simultaneous settlement, I did not know whether immigrants arrived over a period of hours or several days. Further studies using removals and high intruder pressure are needed to clarify the effect of settlement patterns on territory size. For example, food could be added for several weeks before removing residents to ensure a high level of intruder pressure (Chapter 3). Also,
experiments on islands which combine introductions (Boutin & Schweiger 1988) and removals would ensure that there are sufficient animals present to fill vacant areas rapidly.

**Future studies**

In this study, I examined the relationships between food abundance, territorial behaviour and population dynamics of a small, granivorous rodent. Monitoring behaviour directly provided insight into some of the mechanisms which may enable red squirrels to exclude conspecifics under conditions of excess food. Similar experiments on cyclic populations of small mammals (e.g. lagomorphs and microtine rodents) may shed some light on the behavioural changes and the causes of these changes during periodic fluctuations in density. Future studies of species which show cyclic changes in density should conduct realistic manipulations of extrinsic factors such as food or predation while simultaneously examining behavioural changes.
LITERATURE CITED


