# HABITAT USE AND NEST SEARCHING SUCCESS OF RED SQUIRRELS AT A FOREST EDGE.

by

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# ABSTRACT

Recent declines in many songbird populations have been attributed to forest fragmentation (Robinson *et al.* 1995), particularly to elevated rates of nest predation at forest edges. Numerous studies have found an increase in predation rates at forest edges (Paton 1994). However, few studies have tested the processes involved; specifically the habitat use and searching behaviour of individual nest predators. I examined factors influencing the nest searching success of red squirrels (*Tamiasciurus hudsonicus*), a common predator of songbird nests in North American forests. I tested the hypotheses that (1) red squirrels select forest edge habitat, (2) squirrels initially depredate nests opportunistically, (3) with experience, squirrels search actively for nests, and (4) squirrels use an area-restricted search or use nest microhabitat as a search cue to find nests.

I monitored the behaviour and habitat use of individual red squirrels over two summers at a forest-pipeline edge in the south-western Yukon Territory. I tested the influence of nest location, squirrel habitat use and amount of prior nest-finding experience on the survival of 2 artificial nests on each of 40 red squirrel territories. Artificial nests contained Japanese quail and plasticine eggs, and were placed at the base of willow shrubs. I used sand-filled trackboards to record small-scale changes in microhabitat use by squirrels after nests were depredated. Such changes could indicate the use of area-restricted searching or microhabitat-based search cues.

Red squirrels selected forest-pipeline edges in late spring and early summer. Selection of edges by squirrels was highly correlated with a greater abundance of white spruce buds at edges. Although squirrels preferred edges for foraging, I found no difference in the survival of artificial nests between forest edge and interior locations. Smaller scale patterns of habitat use by individuals were also not related to nest survival. However, squirrels found second nests on their territory in one-fifth the time required to find the first nest. Further, survival of the first nest was most closely related to whether a squirrel had depredated a nest the previous year. Squirrels returned to willow nest sites after nests had been found, but did not change their use of similar microhabitats at larger spatial scales. Therefore, neither area-restricted search nor microhabitat-based search cues explain how squirrels efficiently located second nests on their territory.

My results support the hypotheses that red squirrels select forest edge habitat and search actively for nests. Although nest survival was not related to the location of squirrel activity, I cannot reject the hypothesis that predation by squirrels is initially opportunistic. Squirrels may locate nests by chance during random searches when the abundance of traditional foods is low and caching activities are infrequent. I found that squirrels learned to search for nests, thus squirrels could show a functional response to increasing nest densities. Densities of both squirrels and songbirds can change in fragmented landscapes and I discuss how such changes may influence rates of nest predation. Additional tests are required to determine how squirrels learn to search for natural nests. Olfactory cues may be important for this and other mammalian predators. Future studies should continue to focus on individual predators and relate the survival of natural nests to visual and olfactory cues, and to nest density.

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# CHAPTER 1. General Introduction.

The effects of forest fragmentation on animals have been the focus of much recent ecological research. Increases in resource extraction, urban development and agriculture have changed the composition and population sizes of species in fragmented landscapes (Harris 1984, Saunders *et al.* 1991, Andrén 1994). Fragmentation reduces the quantity of forest area and can alter the quality of remaining forest habitat by increasing the amount of exposed forest edge. Declines in populations of neotropical migrant songbirds have received much recent attention (e.g., Hagan and Johnston 1992, Martin and Finch 1995). Loss of forested area and an increase in forest edge habitat are both thought to contribute to declines in these species (Robinson *et al.* 1995).

Nest predation is the primary source of breeding failure in songbirds (Ricklefs 1969, Martin 1992). In fragmented forests, predation rates can be elevated at forest edges (see Paton 1994, and Andrén 1995 for a review). Gates and Gysel (1978) suggested that edges act as an "ecological trap" for songbirds. They argued that songbirds are attracted to the high diversity and abundance of plants and insects at forest edges, but experience lower nest survival at edges due to density-dependent predation. This hypothesis predicts that predators increase their activity at forest edges in response to high densities of nests at edges. Corvids (ravens, crows, jays) and small mammals (raccoons, skunks, squirrels, mice) are frequently cited as primary nest predators (e.g., Paton 1994, Leimgruber *et al.* 1994, Andrén 1995, Bayne and Hobson 1997a). Most of these species have broad diets, and none are thought to specialize on bird eggs. Thus, it has been argued that an active response by predators to increasing nest densities is unlikely (e.g., Angelstam 1986, Storaas and Wegge 1987, Marini *et al.* 1995). Rather, increased predation at edges is thought to be a incidental consequence of a general increase in predator abundance, diversity and activity at forest edges.

Numerous studies have tested patterns of nest predation at forest edges (Paton 1994, Andrén 1995), yet few have focused on the habitat use and behaviour of predators. Predation patterns are explained by correlating nest survival with estimates of predator abundance in forest fragments (e.g., Angelstam 1986, Andrén 1992, Marini *et al.* 1995, Bayne *et al.* 1997a). How predators locate nests has received little direct testing (but see Vickery *et al.* 1992).

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Still, the searching behaviour of predators has been used to explain nesting patterns of birds. Over-dispersion of nests is thought to be a response to predators using area-restricted search (Tinbergen *et al.* 1967). Variation in nesting microhabitat among species is thought to be an adaptation against the use of specific nest site search cues by predators (Martin 1988, Martin 1993). However, in one of the few tests of predator behaviour, Vickery *et al.* (1992) found no evidence to indicate that skunks searched for nests actively; instead skunks appeared to depredate nests opportunistically. Clearly, more studies on the habitat use and searching behaviour of nest predators are needed to further test these hypotheses.

This study has two objectives: (1) to examine the habitat use and behaviour of individual red squirrels at a forest edge, and (2) to test whether these activity patterns or prior nest-finding experience influence the success of squirrels searching for artificial songbird nests. Red squirrels are abundant in conifer forests in North America (Banfield 1974, Nowak 1991), and are frequently cited as a primary nest predator (e.g., Bayne and Hobson 1997a, 1997b, Darveau *et al.* 1997, Sieving and Willson 1998, Sloan *et al.* 1998). Red squirrels defend exclusive territories year round (C. Smith 1968, Rusch and Reeder 1978, Gurnell 1984) thus survival of nests on known territories can be related to characteristics of individual predators. Though their diet focuses on conifer seeds (Brink and Dean 1966, M. Smith 1968), red squirrels are quick to take advantage of alternate food sources. There is much scientific and anecdotal evidence for the carnivorous and predatory nature of these and other squirrels (e.g., Callahan 1993). In fact, past research at Kluane, Yukon, my study site, found red squirrels to be the primary predator of juvenile snowshoe hares (O'Donoghue 1994, Stefan 1998).

I tested four hypotheses regarding red squirrel habitat use and searching behaviour for nests: 1) red squirrels select forest edge habitat within their territory; 2) predation on artificial nests is, initially, opportunistic, and nest survival is related to the habitat use of red squirrels; 3) red squirrels learn to search for artificial nests within their territory and; 4) red squirrels use area-restricted search or nest microhabitat search cues to locate successive nests. In Chapter 2, I examine the use of forest edges by red squirrels and describe changes in the behaviour of squirrels over the summer. I relate edge use by squirrels to the abundance of food at edges, territorial behaviour and predation risk at a forest edge. In Chapter 3, I relate the searching success of individual squirrels to their habitat use, behaviour and prior experience, and I

compare nest survival among forest edge and interior locations. I show that squirrels learn to search for nests, and discuss the implications of this finding for the nesting success of songbirds in fragmented forests.

**CHAPTER 2. Habitat selection and behaviour of red squirrels at a forest edge.**

**INTRODUCTION**

Edge effects are a series of abiotic and biotic changes that occur when two different habitats meet (Odum 1971, Saunders *et al.* 1991, Murcia 1995). Interest has focused on changes in wildlife at forest-clearing edges as forest become fragmented due to resource extraction, agriculture and urban development (Harris 1988, Yahner 1988). Early studies, primarily on game species, suggested that species show a positive response to the creation of forest edges (e.g., Leopold 1933). More recent work has emphasized negative aspects of fragmentation, particularly with respect to declines in neotropical migrant songbirds (Robinson *et al.* 1995), and elevated rates of nest predation and parasitism at forest edges (Gates and Gysel 1978, Paton 1994).

Less is known about the behavioural response of small mammals to forest edges. Many small mammals depredate songbird nests (e.g., DeGraaf 1995, Haskell 1995, Fenske-Crawford and Niemi 1997) and could contribute to increased nest predation at edges. How small mammals respond to forest edges likely depends on the species and landscape. Species relying on forested habitat may avoid edges due to increased predation risk (Bowers and Dooley 1993, Thorson *et al.* 1998) or lack of food (Mills 1995). Edge avoidance may be stronger in recently logged forests than in agricultural landscapes where crops or refuse attracts foraging activity (Heske 1995, Sheperd and Swihart 1995). However, species often show inconsistent responses to forest edges. For example, southern red-backed voles (*Clethrionomys gapperi*), have shown positive (Kirkland 1990), negative (Sekgororoane and Dilworth 1995) and no response (Bayne and Hobson 1998) to forest edge or cleared habitat.

Most of the above studies have tested the population level response of small mammals to forest edges using trapping data. Few studies have examined the response to edges at an individual level (but see Bowers *et al.* 1996). Using species abundance to infer habitat quality or preference can be problematic (Van Horne 1983). Annual fluctuations in density are common in many small mammal populations (Taitt and Krebs 1985, Boutin *et al.* 1995) and density may influence the number of dispersing animals and occupancy of poor quality habitats (Stenseth and Lidicker 1992). Small mammal populations can be unnaturally high in isolated

forest patches if the surrounding matrix acts as a dispersal barrier (i.e. "fence effect" Krebs *et al.* 1969, Wolff *et al.* 1997). Seasonal changes in the diet and reproductive behaviour of species may also lead to variation in habitat use among and within seasons.

Here I examine habitat selection by individual red squirrels at a forest edge created by an abandoned pipeline. Specifically, I tested the hypothesis that red squirrels selected forest edge habitat within their territory. Red squirrels rely on coniferous seeds through winter and early spring (Brink and Dean 1966, C. Smith 1968, M. Smith 1968). They are found in almost all conifer forests in Canada, and in the north-eastern and Rocky Mountain regions of the USA (Nowak 1991). In northern areas, these forests are becoming increasingly fragmented by seismic lines, roads and pipelines (Strong 1986). Although they are considered a conifer forest specialist (Brink and Dean 1966, Smith 1970), I predicted that red squirrels would select this edge for three reasons. First, squirrels use a variety of foods in summer when few cones are available (C. Smith 1968, Ferron *et al.* 1986, Wauters *et al.* 1992). Because plant diversity and growth can be high at forest edges (Ranney *et al.*, Matlack 1993, Murcia 1995), edges may provide squirrels with profitable and varied foraging opportunities. Second, red squirrels defend individual territories throughout the year (C. Smith 1968, Rusch and Reeder 1978, Gurnell 1984) and territories are often bounded by forest edges. Thus, squirrels could use edges when defending or demonstrating territory boundaries or for vigilance activities. Finally, in comparison to edges adjacent to large clearings, predation risk at a forest-pipeline edge may not be high enough to deter squirrel activity. Squirrels would rarely be greater than 8 m from cover at any point in the pipeline clearing, and foliage cover may be particularly high at both pipeline borders.

To determine habitat use, I monitored the behaviour of individual squirrels over 2 spring/summer seasons. I tested for selection or avoidance of five habitat categories within a squirrel territory (forest edge, forest interior, midden, shrub/pipeline and general forest) and I describe changes in habitat use over the spring/summer season. To test my hypotheses for edge selection, I also examined: (1) within season changes in the activity budget and diet of red squirrels, (2) differences in squirrel behaviour among habitat categories, and (3) differences in bud biomass, cone abundance, and foliage cover of white spruce (*Picea glauca*) between the forest edge and forest interior portions of red squirrel territories.

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## METHODS

### Study area

Research was conducted from May to July, 1996 and May to August, 1997 in boreal forest in the Shakwak valley near Kluane Lake in the south-western Yukon Territory (61°N, 138°W). The area is dominated by white spruce forest with a sparse understory of grey willow (*Salix glauca*), bog birch (*Betula glandulosa*) and low growing vegetation (e.g., *Festuca spp.*, *Arctostaphylus uva-ursi, Lupinus arcticus*). The valley also contains several bogs and ponds, patches of dense willow (*Salix spp.*) and birch shrubs, and stands of balsam popular (*Populus balsamifera*) and aspen (*Populus tremuloides*) (Douglas 1974). An abandoned oil pipeline runs the length of the valley and I used the pipeline-forest border as a forest edge habitat in this study. The pipeline was created in the mid 1950's and remains approximately 15 m wide. The pipeline is dominated by grass species and low growing herbaceous plants. Willow, birch and soapberry (*Shepherdia canadensis*) shrubs dominate the 0-8 m border between the pipeline and forest. A 15 m wide abandoned dirt and gravel road, with a similar forest edge border, also served as a forest edge in some squirrel territories.

I studied red squirrels on and adjacent to two 36 ha study grids previously set up as control sites as part of the Kluane Boreal Forest Ecosystem Project (e.g., Boutin *et al.* 1995). The two 600 x 600 m grids were approximately 1.5 km apart. Each grid was marked at 30 m intervals with wooden stakes and coloured flagging displaying grid coordinates; grid coordinates were based on the division of each 30 m interval into ten 3 m units. Both grids were bisected by the abandoned pipeline and were dominated by white spruce forest. Tree height on the grids was approx. 10-15 m. Most red squirrels and squirrel middens on these grids were already identified in separate studies (e.g., Humphries and Boutin 1996).

### Behaviour and territory use of red squirrels

I identified the red squirrels owning territories in May of each year through live-trapping and behavioural observation of individuals. I located squirrel middens within 40 m of the abandoned pipeline and trapped for midden owners using Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin) baited with peanut butter. Unmarked squirrels were marked with a numbered metal ear tag (No. 1 monel tags, National Band and Tag Co., Newport, Kentucky) and coloured wire was attached to these tags to facilitate

identification of individuals during behavioural observations. The weight, sex and reproductive condition of each squirrel was recorded and squirrels used for behavioural study were fitted with a radio-transmitter collar (approx. 3.6 g, Model No. PD-2C, Holohil Systems Ltd., Woodlawn, Ontario). Thirty-three middens were censused in 1996 and 40 middens were censused in 1997. In 1996, I included one new midden that was outside the existing study grid and had not previously been censused. Eight new middens were censused in 1997. Only 5 of the 33 squirrels in 1996, and 9 of the 40 in 1997, had not been marked in previous years. Territory fidelity and summer survival were measured by trapping or observing midden owners in August of each year.

I sampled the behaviour of 33 squirrels in 1996 and 10 squirrels in 1997 using point sampling and focal animal sampling techniques (Martin and Bateson 1993). Each squirrel was initially located by sight, sound or radio telemetry and the location and behaviour of that initial "first seen" point recorded (Appendix 1). I estimated the location of the squirrels to the nearest 3 m unit by referring to the marked stakes and flagging on the grids. After allowing a 1-10 minute habituation period, I conducted a 4 min (1996) or 10 min (1997) sample of the focal animal, recording instantaneous samples of its behaviour and location every 30 seconds.

Each squirrel was observed at least once in every hour between 0600 and 1230 hrs during each sampling period. Squirrels are most active during morning hours (C. Smith 1968) and preliminary study in 1996 suggested that red squirrel predation on artificial nests was highest during this period. I collected as many behavioural samples per squirrel per day as possible. I left at least one hour between each sample for an individual to ensure that samples were independent. Observations were conducted from May 14 to July 22 in 1996, and during three sampling periods in 1997: May 10-31, June 25-July 19, and August 7-18.

Behavioural analyses were limited to 21 of the 33 squirrels observed in 1996 and to 9 of the 10 squirrels observed in 1997. Squirrels excluded from analyses either failed to habituate to observers (n=10, indicated by alarm vocalizations, vigilance or traveling away from the observer) or died or dispersed during the study (n=3). Behavioural summaries were based on observations where squirrels were not in nests and their location was known to the observer. I used 9 general activity and location categories (foraging, feeding or caching in a white spruce (tree); foraging, feeding or caching on the ground; traveling in a tree; traveling

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on the ground; active on a midden; active on a willow; vigilant; vocalizing; and other) and 11 food classes (spruce bud, willow, old spruce cone in tree, old spruce cone on ground, new cone in tree, new cone on ground, fungi in tree, fungi on ground, other in tree, other on ground, and non-food) (Appendix 2). I hereafter refer to all foraging, feeding and caching activities as foraging.

Both the "first seen" point samples and the focal samples were used to summarize and compare squirrel behaviour. I used point samples to analyse the habitat use of red squirrels within their territory. The focal samples were used to calculate overall activity budgets and to compare activity budgets among time periods. For each sample I calculated the proportion of time spent in each of the behaviour categories. These proportions were then averaged over all focal samples for each squirrel. A total of 383 focal samples (37.2 hours) and 622 point samples were used for analysis in 1996; 336 focal samples (45.3 hours) and 426 point samples were used in 1997.

**Habitat availability within territories**

I recorded and mapped grid coordinates (to the nearest 3 m) of the pipeline and tree edge at 10 m intervals along the forest-pipeline boundary within each of the study grids. I classified the pipeline edge as the point where the vegetation changed from low grass, which was dominant within the pipeline, to the shrub and tall herb vegetation dominating the pipeline border. The grid coordinate of the tree (>3 m tall) nearest to the pipeline was recorded as the forest or tree edge. Squirrel territory boundaries were determined by plotting and connecting the outer grid coordinates of squirrel behaviour observations. This method is similar to the commonly used minimum-convex-polygon (MCP) procedure (Kie *et al.* 1994). However, I first excluded points where squirrels were interacting with neighbouring squirrels or within the territory of another individual. I superimposed territory borders on the forest and pipeline edge maps and assumed that each territory extended half-way into the pipeline clearing, even if squirrels were not observed in that area.

I divided each squirrel territory into five habitat classes: forest edge territory border (forest edge), interior forest territory border (forest interior), midden, shrub/pipeline and general forest (Figure 2.1). Edge and interior classes included all forested habitat within 9 m of the tree edge and opposite territory border, respectively. I used the interior territory border

**Forest interior** territory border (9m in width)

**General forest**

**Midden**

red squirrel territory border

tree edge

**Forest edge** territory border (9m in width)

**Shrub/ Pipeline**

9m
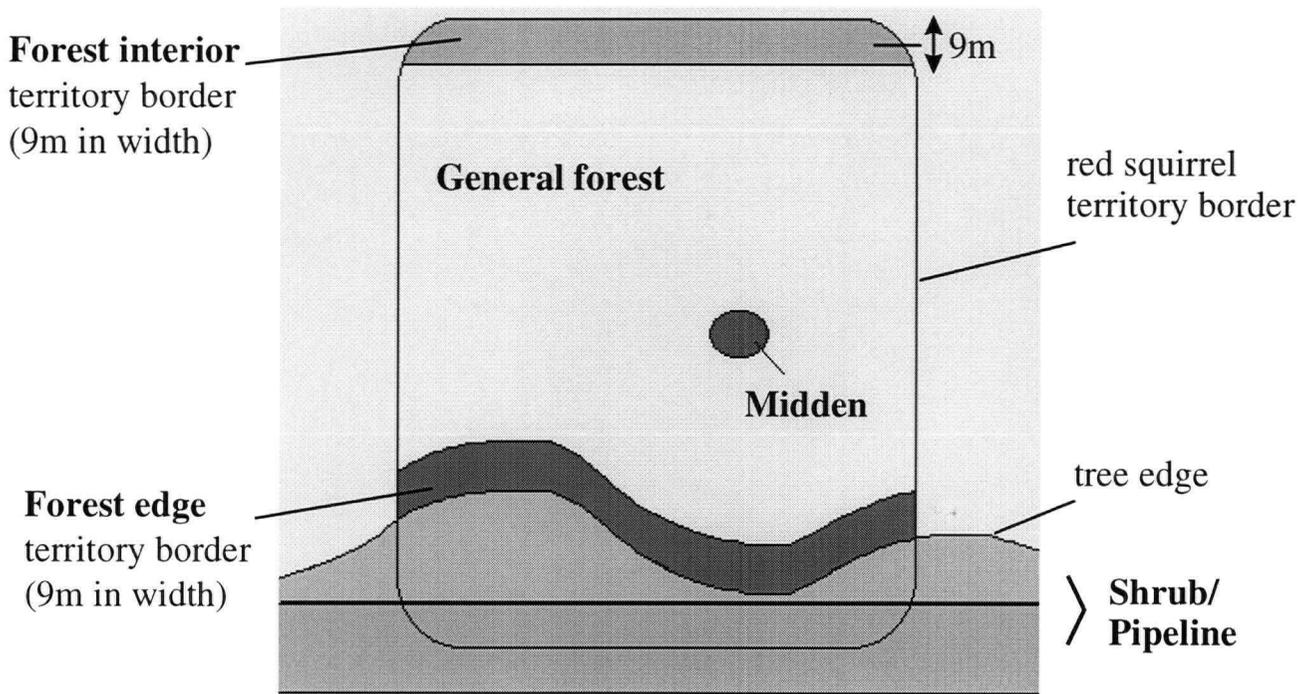
**Figure 2.1.** Diagram of habitat classification within red squirrel territories at a forest-pipeline edge (not to scale). Each squirrel territory was divided into 5 habitat classes: forest edge, forest interior, midden, shrub/pipeline and general forest. See text for a full description of habitat categories.

to control for any specific territory boundary behaviours that might occur in the forest edge habitat. Shrub/pipeline habitat includes all non-forested area from the tree edge to half way into the pipeline. I considered midden habitat to be a 3 m x 3 m area centered on the grid coordinates for the midden(s) on each territory. Middens or portions of middens within the forest edge or interior categories were classified as midden rather than edge or interior habitat. The remaining area within the territory was classified as general forest. I digitized the territory and habitat borders for each territory map and used AREAS computer program (written by A. Blachford, Department of Zoology, University of British Columbia, 1996) to calculate the area of each habitat. The proportion of available habitat was determined for each squirrel by dividing the area of each habitat by the total territory size.

**Habitat use within territories**

I analysed red squirrel habitat use by calculating a selection coefficient and its 95% confidence interval (Manly *et al.* 1993) for each of the five habitat categories within squirrel territories. The selection coefficients were calculated as:

$$w_i = u_{it} / \sum_{j=1}^{n} p_{ij} \, u_{tj}$$

where $w_i$ is the selection coefficient for habitat $i$, $u_{it}$ is the sum total of counts ("first seen" point samples) in habitat $i$ for all squirrels, $n$ is the number of squirrels, $p_{ij}$ is the proportion of habitat $i$ in the territory of squirrel $j$, $u_{tj}$ is the total number of observations of squirrel $j$.

The Bonferonni corrected 95% confidence interval for each selection ratio was calculated as:

$$w_i \pm z_{\alpha/2I} \, SE(w_i)$$

where $I$ is the number of habitat categories, $z_{\alpha/2I}$ is the critical value of the normal distribution with an upper tail probability of $\alpha/2I$, and $SE(w_i)$ is the standard error of the selection coefficient for habitat $i$. Selection coefficients represent the ratio of observed use of each habitat to that expected if squirrels used habitat in proportion to its availability within each territory. Coefficients with lower confidence intervals greater than 1.0 indicate significant selection for that habitat, upper confidence intervals less than 1.0 indicate significant avoidance (Manly *et al.* 1993).

## Sampling of white spruce

I measured bud biomass, cone abundance and foliage cover of white spruce on forest edge and forest interior transects on each study grid. Forest edge transects were located at both the north and south tree edge. Forest interior transects ran parallel to the edge and were 60 m from edge transects, the approximate width of red squirrel territories at this site (pers. obs., Price 1994). Each transect had 10 sampling stations 60 m apart to allow for paired analysis between stations at forest edges and interiors and between north and south facing edges. Bud biomass was sampled between May 22 and May 30, 1996, and spruce cover and cone abundance between August 11 and August 17, 1996.

I measured bud biomass by pruning branch tips at 5 heights (approx. 1.5-7 m) from each of the 3 closest trees (>3 m in height) at each station. Vegetative or reproductive buds forming on the past three years growth were removed and weighed. I averaged the total biomass from each of the three trees at each station for analysis. All samples were collected within 24 hours on each grid; analysis was limited to samples where buds were weighed no later than 48 hours after collection (north transects on one study grid only).

I measured spruce foliage cover and cone abundance on the two closest trees (>4 m in height) at each station. Cover was estimated by recording the percent of edge-facing trunk greater than 1.5 m in height that was visible when standing 2 m from the tree. Cone abundance was measured by counting the number of newly developed cones within the top 3 m on the edge-facing side of each tree. Individual tree measurements were averaged for an overall station estimate.

## Sampling errors

When studying animal behaviour, researchers must be aware of potential biases in their sampling and analysis methods. The location and behaviour of squirrels in this study may have been affected by an individual's reaction to my presence (e.g., moving towards or away from me). Several factors may have also influenced how quickly and precisely I could locate the squirrels. I may have been better able to detect squirrels at forest edges, when squirrels were vocalizing, or during calm, sunny weather. I attempted to minimize such biases by locating squirrels as quickly and quietly as possible, approaching territories from various directions and moving towards the midden, and by not sampling behaviour during rainy or windy conditions.

My selection coefficients could also be influenced by errors in territory mapping. A bias in my mapping method and low sample sizes would underestimate territory size. This underestimate would reduce ratios of habitat use to availability for forest interior and general forest habitats, and increase ratios for forest edge, midden and shrub pipeline habitat. Finally, my selection coefficients should be interpreted with caution as there may be inherent difficulties with measuring resource selection (see Johnson 1980, Thomas and Taylor 1990, Orians and Wittenberger 1991). For example, low selection coefficients may be misinterpreted as avoidance. When an animal selects strongly for one habitat, use of remaining habitats will automatically be low, even if the animal is not actively avoiding these areas.

## RESULTS

### Use of forest edges and habitats within territories

In both 1996 and 1997 red squirrels selected forest edge and midden habitat within their territory. Shrub/pipeline habitat was strongly avoided, general forest habitat was used less than its availability, and forest interior habitat was used in proportion to (1996, May 1997) or less than (June-August 1997) its availability within territories (Figures 2.2-2.3, Appendix 3). Dividing the 1997 data into the three time periods shows decreasing forest edge and forest interior use, and an increase in general forest use, as the season progressed (Figure 2.3). Use of edges by squirrels was nearly double that expected through the summer, but selection of edges was no longer statistically significant in August. Squirrels used the forest interior in proportion to its availability in May, but, by August, squirrels had decreased their use of interior habitat by half. Use of general forest habitat was roughly half that expected in early summer, however, squirrels used this habitat in proportion to its availability by August. Squirrels used midden habitat over 16 times more frequently than expected, and used shrub/pipeline habitat nearly 6 times less than expected through all periods in 1997.

### Red squirrel activity budgets and intra-seasonal variation

Red squirrels spent the majority of their time (64-82%) foraging (i.e. feeding, foraging or caching) in both 1996 and 1997 (Figures 2.4-2.5). In 1997, the average frequency of these activities decreased from 82.4% per squirrel in May to 64.9% in August (Figure 2.5). This
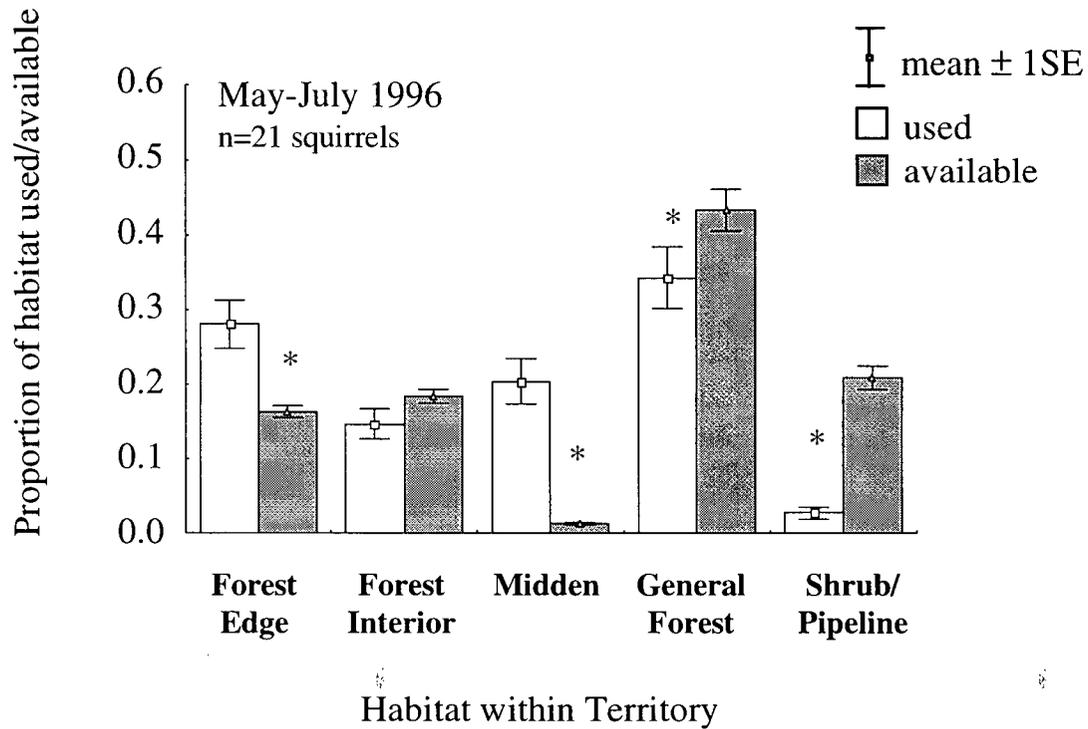
**Figure 2.2.** Use vs. availability of habitat classes within red squirrel territories, May 14 - July 22, 1996 (averaged over all squirrels). * Indicates significant selection or avoidance of habitats based on the 95% confidence interval of the selection coefficient for each habitat (see text and Appendix 3).

**Figure 2.3.** Use vs. availability of habitat classes within red squirrel territories during 3 sampling periods in 1997. * Indicates significant selection or avoidance of habitats based on the 95% confidence interval of the selection coefficient for each habitat (see text and Appendix 3).

a) May (n=8 squirrels)

mean ± 1SE
☐ used
▨ available

b) June/July (n=9)

c) August (n=9)

Edge Border   Interior Border   Midden   General Forest   Shrub/Pipeline

Habitat within Territory

Proportion of habitat class used/available

15
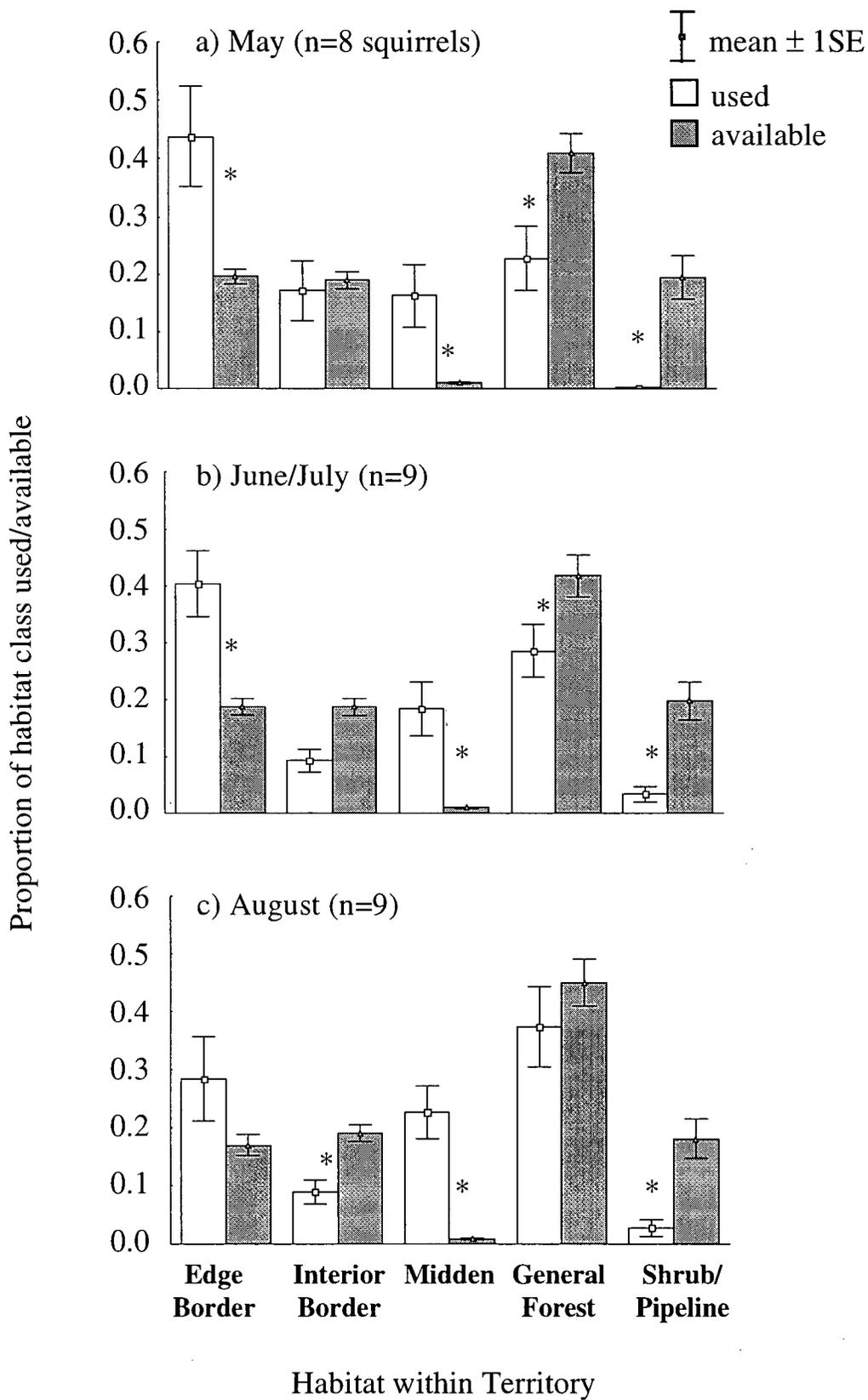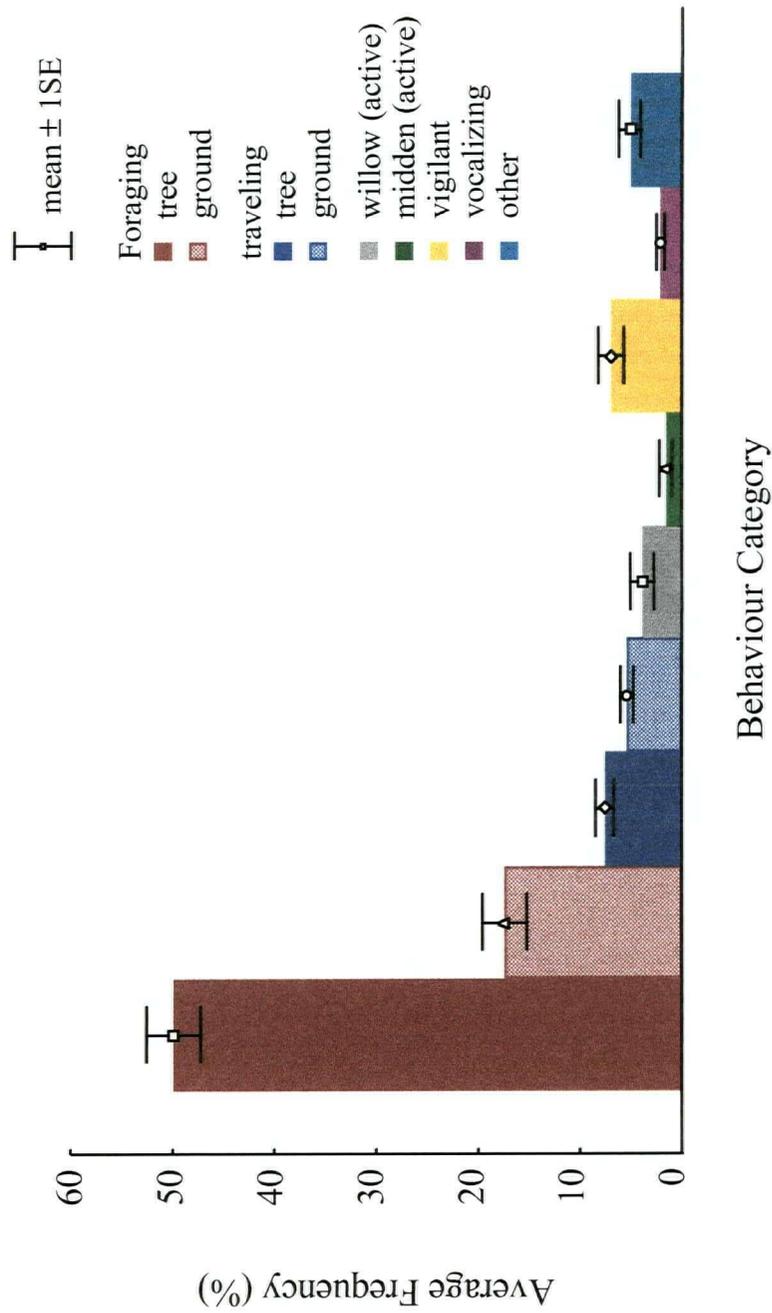
**Figure 2.4.** Average frequency of red squirrel behaviour categories between May 14 and July 22, 1996 (n=21).
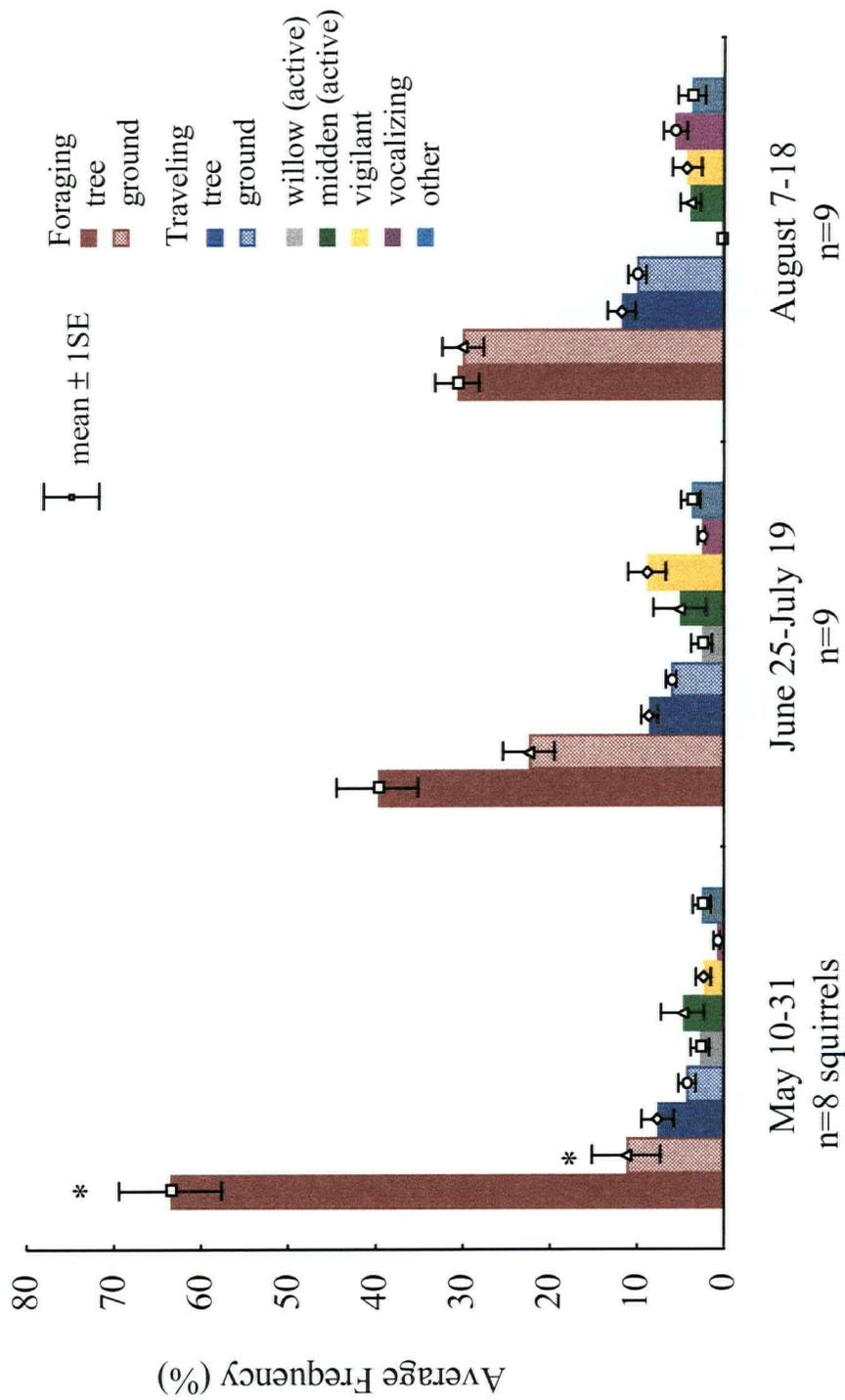
**Figure 2.5.** Average frequency of red squirrel behaviour categories among sampling periods in 1997. * Frequency of foraging in trees and on the ground in May differed from frequencies in June/July and August, Spjotvoll/Stoline Post Hoc test (Tukey's HSD for unequal sample sizes) $p < 0.05$.

drop in foraging was associated with an increase in traveling from 11.9% in May to 21.8% in August. There was little change in the frequency of vocalization, vigilance and "other" behaviours among periods in 1997. Activity budgets for May to July periods were very similar in 1996 and 1997.

Squirrels shifted the location of foraging activities as the 1997 season progressed (Figure 2.5). In late spring, squirrels foraged over 5 times more frequently in spruce trees than on the ground. By August, however, foraging in trees and on the ground occurred with nearly equal frequency. Foraging on the ground had nearly tripled since May, and foraging in trees had decreased by nearly one half (Figure 2.5). Squirrels did not show a similar shift in the location of traveling activity; traveling in trees remained slightly more frequent than ground traveling through the three periods.

Squirrels probably changed the location and frequency of their foraging activities in relation to the type of foods used over the season (Table 2.1). In spring 1997, squirrels spent over half of their time foraging on vegetative and reproductive buds of white spruce. Each of the remaining 5 food categories had average frequencies of less than 10%. In the June/July period, squirrels were using foods in all 10 food categories, with "other" foraging in trees (e.g., witches' broom, insects, unknown items in tree) occurring with the highest frequency. In August, squirrels divided their time between harvesting and caching new spruce cones and fungi, and foraging for other ground and tree foods. When using new cones and fungi, squirrels spent nearly equal amounts of time in trees and on the ground. Squirrels spent most time on "other" ground food items in late summer.

**Behaviour of squirrels among and within habitats**

I tested for differences in squirrel behaviour among habitats by comparing both overall activity budgets and individual behaviours. Sample sizes were low for midden and shrub/pipeline habitats and during May and August 1997. Thus, I limited statistical analyses to only the forest edge, forest interior and general forest habitats and used only the June/July period when comparing overall activity budgets in 1997. My null hypothesis was that behaviours occur with equal frequency across all habitats. Therefore, for goodness of fit comparisons, I calculated expected frequencies in each habitat by multiplying the average frequency of a given behaviour (over all five habitats) by the total number of squirrel

**Table 2.1.** Average frequency of red squirrel activities categorized by food type in 1996 and during three time periods in 1997. Frequencies were based on individual focal samples and an average calculated per squirrel per time period; individual squirrel averages were used to calculate overall averages and standard errors.

| Food Type and Substrate | Average Frequency (±1SE) % | | | |
|---|---|---|---|---|
| | May14-July17 1996 | May 10-31 1997 | June 25 - July 19 1997 | August 7 - 18 1997 |
| Spruce buds (tree) | 30.8 (4.4) | 57 (7.3) | 0.8 (0.6) | 0 (0) |
| Willow | 3.3 (1.1) | 2.8 (1.2) | 2.6 (1.2) | 0 (0) |
| Old cones[a] | | | | |
| Ground | 6.7 (1.4) | 9.2 (3.6) | 7 (3.6) | 0.5 (0.5) |
| Tree | 4.4 (1.7) | 1.5 (0.9) | 1.5 (1) | 0 (0) |
| New cones[a] | | | | |
| Ground | 0.8 (0.4) | 0 (0) | 0.9 (0.3) | 7.7 (2.7) |
| Tree | 9.0 (2.5) | 0 (0) | 7.8 (2.2) | 11.3 (1.7) |
| Fungi[b] | | | | |
| Ground | 0.9 (0.3) | 0 (0) | 3.7 (0.9) | 10 (0.9) |
| Tree | 0.2 (0.1) | 0 (0) | 1 (0.3) | 11.5 (1.7) |
| Other[c] | | | | |
| Ground | 10.4 (1.5) | 6.8 (2.5) | 16.3 (2.7) | 15.3 (2.5) |
| Tree | 7.4 (1.3) | 5.1 (3.1) | 27.7 (4.3) | 8.6 (1.5) |
| Non-food activity | 26.0 (1.9) | 17.6 (3) | 30.7 (3.2) | 35.1 (3.8) |
| No. food items used (≥) | 17 | 8 | 11 | 5 |
| N - # of squirrels | 21 | 8 | 9 | 9 |
| (focal samples/sq) | (17.4) | (7.8) | (18.2) | (12.2) |

[a] old cones refer to cached cones from the previous year, new cones to cones produced that year

[b] fungi includes mushrooms and underground truffles

[c] "other" includes: unknown or unsuccessful foraging, vegetation, invertebrates, small vertebrates, berries, and trembling aspen

observations in that habitat. I performed goodness of fit tests only when >20% of expected and observed counts were greater than 5 (Sokal and Rohlf 1995). I used Bonferonni adjusted alpha levels (0.05/number of behaviour comparisons) when analysing more than one behaviour category.

The distribution of squirrel activities differed significantly among the forest edge, forest interior and general forest habitats in 1996 (G = 21.13, df=12, p=0.05). Squirrel behaviour differed most between edge and general forest habitat (G=13.12, df=6, p=0.04). Only tree foraging differed from expected average frequencies within habitats (Table 2.2, Appendix 4). This difference was primarily due to squirrels concentrating tree foraging in forest edge habitat. Comparing the use of 6 food types within habitats revealed that only bud and new cone foraging differed from expected values within habitats (Table 2.2, Appendix 4). Again, squirrels concentrated these activities in forest edge habitat, though bud foraging was also higher than expected in the forest interior. Squirrels foraged for willow, old cone, other ground and other tree foods at the expected average frequencies in the forest edge, interior and general forest habitats (Appendix 4).

The distribution of squirrel behaviour among habitats in 1997 was similar to that seen in 1996 (Table 2.2, Appendix 5), though the differences among habitats were not as strong (G=15.29, df=12, p=0.23). Squirrels foraged in trees more than expected in forest edge and forest interior habitat. Also, squirrels concentrated new cone and bud foraging in forest edge and interior habitat, respectively. However, none of these patterns of selection were statistically significant (Appendix 5). Sample sizes were low in May 1997, when tree and bud foraging was most frequent, and were low for the interior habitat in general.

**Foliage cover and production of white spruce**

Spruce bud (primarily vegetative bud) biomass at the forest edge was 3 times higher than in the forest interior (Table 2.3). Foliage cover comparisons differed between north-facing and south-facing transects. Lateral spruce cover was significantly (20 percentage points) higher at forest edge than interior transects on the south-facing side of the pipeline. I found no difference in cover between north-facing edge and interior transects (Table 2.3). Cover estimates were 1.3 times higher on south-facing than north-facing edge transects (Wilcoxon Matched Pairs test, Z=3.18, N=20, p=0.001), but there was no significant

**Table 2.2.** Comparison of observed and expected frequencies of red squirrel behaviours among forest edge, forest interior and general forest habitats for May 14 - July 22, 1996, and May 10 - August 18, 1997. Results are presented only for activities where observed and expected frequencies differed in 1996 (see Appendices 4-5 for all activities). The null hypothesis is that each activity occurs with equal frequency across habitats. Thus, expected frequencies are the average frequency of each activity over all 5 habitat classes.

| | Observed Frequency (%) | | | Expected (%) | $X^2$ (Edge + Interior + General forest)[a] | p |
|---|---|---|---|---|---|---|
| | Edge | Interior | General Forest | | | |
| **1996** | | | | | | |
| **General categories** [b] | | | | | | |
| Tree foraging | 38.7 | 37.2 | 23.0 | 28.6 | 10.3 (6.0 + 2.0 + 2.3) | 0.006 |
| **Food categories** [c] | | | | | | |
| Spruce buds (tree) | 23.2 | 24.4 | 10.0 | 16.3 | 13.1 (5.0 + 3.1 + 5.0) | 0.001 |
| New cones | 12.5 | 2.6 | 6.7 | 7.0 | 9.5 (7.3 + 2.2 + 0.03) | 0.009 |
| N | 168 | 78 | 209 | | | |
| **1997** | | | | | | |
| **General categories** [d] | | | | | | |
| Tree foraging | 43.3 | 45.2 | 33.3 | 36.0 | 3.0 (2.2 + 0.7 + 0.1) | 0.226 |
| **Food categories** [c] | | | | | | |
| Spruce buds (tree) | 14.0 | 23.8 | 3.9 | 10.7 | 6.3 (1.0 + 3.3 + 2.0) | 0.043 |
| New cones | 10.2 | 4.8 | 5.4 | 6.2 | 4.6 (4.2 + 0.1 + 0.3) | 0.100 |
| N | 157 | 42 | 129 | | | |

[a] contribution of individual habitat comparisons to total $X^2$ value; [b] $\alpha=0.008$ (Bonferonni adjustment for comparison of 6 behaviour categories); [c] $\alpha= 0.01$ (5 comparisons); [d] $\alpha=0.013$ (4 comparisons)

**Table 2.3.** Cover and production estimates of white spruce at forest-pipeline edges and on forest interior transects (60 m from forest edge). Bud samples were collected and weighed in May 1996, and cover and cone abundance measured in August 1996. Wilcoxon Matched Pairs results are presented for transects on the north-facing and south-facing side of the pipeline.

| | Mean ($\pm$1SE) Sampling Station Averages | | | | |
| | Forest Edge | Forest Interior | N | Z | p |
| --- | --- | --- | --- | --- | --- |
| **Bud biomass (g)** | | | | | |
| south-facing | 3.3 (0.4) | 1.1 (0.3) | 11 | 2.93 | < 0.01 |
| **Lateral cover (%)** | | | | | |
| south-facing | 86.3 (3.0) | 66.2 (5.2) | 20 | 3.28 | < 0.01 |
| north-facing | 69.0 (3.6) | 58.5 (4.5) | 20 | 1.63 | 0.10 |
| **Cones/tree** | | | | | |
| south-facing | 32.0 (8.1) | 40.8 (7.2) | 20 | 0.85 | 0.40 |
| north-facing | 10.4 (3.0) | 23.4 (6.9) | 20 | 1.89 | 0.06 |

difference between interior transects north and south of the pipeline (Z=1.33, N=20, p=0.18). Cone abundance in the forest interior was higher than at the forest edge (Table 2.3). However, there were 1.7 to 3 times more cones on the south-facing than north-facing side of the pipeline (edge transects Z=2.19, N=20, p=0.03; interior transects Z=1.85, N=20, p=0.06).

## DISCUSSION

Red squirrels selected for forest edge habitat within their territory in late spring and early summer. Selection of edges in spring is due to frequent use of forest edges for foraging for new cones and spruce buds. Bud biomass was 3 times higher at forest edge than in the interior forest. Squirrels decreased their use of edges over the summer as they shifted from foraging for spruce buds and other tree foods in spring, to foraging for and caching fungi, spruce cones and other ground-based foods later in summer.

These results support my original hypothesis that red squirrels select forest edges. I proposed three mechanisms for edge selection: greater foraging opportunities at forest edges, concentration of territorial and vigilance behaviour at a territory border and relatively low predation risk at forest-pipeline edges. I first discuss the general activity patterns of red squirrels before considering the potential mechanisms of edge selection in more detail.

### Red squirrel activity budgets and general territory use

Aside from selecting edge habitat, red squirrels showed strong selection for midden habitat and tended to use forest interior, general forest and shrub/pipeline habitats less than expected based on their availability. Most of these results are expected from previous knowledge of red squirrel behaviour. A concentration of caching, nesting and feeding activity at a central cache site (i.e. midden) is characteristic of red squirrels (C. Smith 1968, Gurnell 1984). Strong avoidance of clearings also has been reported in European red squirrels (Andrén and Delin 1994) and is expected if predation risk is higher in clearings due to lack of cover (Lima et al. 1985, Thorson et al. 1998). Non-uniform use of territories is also not surprising. Red squirrels are known to concentrate foraging and feeding activities in habitats (Benhamou 1996) or specific locations (Lair 1987) that are profitable or that potentially lower predation risk (Yahner 1987). Although use of general forest was lower than expected, it was not necessarily uniform.

Infrequent use of forest interior borders contradicts my initial prediction that squirrels regularly use territory borders. Vocalizations, which are often used to when defending or advertising territories (Smith 1978, Lima *et al.* 1985), occurred at the expected average frequency in all habitats. Price 1994 suggested that squirrels may respond more strongly to intruders at territory borders, but others report that rattle calls (Smith 1978, Lair 1990) and scent marking (Ferron and Ouelett 1988) occur throughout a squirrel's territory. Red squirrels defend exclusive territories year round (C. Smith 1968, Rusch and Reeder 1978, Gurnell 1984). If territory borders are "known", there may not be a need for squirrels to patrol borders. Periodic rattle calls may be a sufficient, and economical, way to advertise territory occupancy (Lair 1990).

Red squirrels spent most of their time feeding, foraging or caching. In 1997, the location of foraging activities shifted from primarily in trees in May to a relatively equal division between tree and ground locations in August. This shift was associated with seasonal changes in the type of foods used by squirrels. Squirrels ate spruce buds in spring, and ate or cached fungi and cones later in summer. Other studies also have shown that squirrels devote most activity to foraging (50-80% Ferron *et al.* 1986, 51% Benhamou 1996, 50% Humphries 1996). Seasonal changes in the ratio of ground to tree foraging differed among these studies and my own (Ferron *et al.* 1986, Benhamou 1996). However, ground to tree ratios were still related to the location of abundant food in each study area.

**Selection of forest edges**

As predicted, red squirrels selected forest edge habitat, though they did so only in late spring to early summer. I suggested three, non-exclusive, hypotheses for selection of this forest-pipeline edge: increased food resources at edges, increased territorial behaviour at edges and relatively low predation risk. As territorial behaviours were not more frequent at the forest edge, selective use of edges cannot be explained by the second hypothesis.

Use of forest edges by squirrels was strongly associated with increased spruce bud abundance at forest edges. This result is consistent with my first hypothesis. Squirrels selected edge habitat in late spring and early summer. At this time, squirrels spent most of their time feeding on spruce buds, and concentrated this activity in edge habitat. Cone caches are often low by late spring and vegetative buds are an important alternate food source for

squirrels during this period (Rusch and Reeder 1978, Ferron *et al.* 1986, Wauters *et al.* 1992). It is not surprising that squirrels would respond to a productive food source. As mentioned above, squirrels frequently alter their habitat use and foraging activity according to the availability and abundance of both traditional and alternate foods (Ferron *et al.* 1986, Wauters *et al.* 1992, Benhamou 1996). Although foods such as willows, grass and low growing vegetation were abundant outside the forest canopy, overall use of these items by squirrels was low. Still, willows and grass may be important resources for squirrels at certain times (e.g., willow buds, insect outbreaks), or when they are constructing nests.

Increased sunlight is a common explanation for higher plant diversity and production at forest edges (Ranney *et al.* 1981, Murcia 1995). As bud production in conifers is generally correlated positively with temperature (Ross 1989, Bonnet-Masimbert and Webber 1995), increased sunlight likely also explains the increased spruce bud biomass I report here. Although I found no difference in cone abundance between forest edge and interior transects, both cone abundance and foliage cover were greater at south-facing than north-facing forest edges. Warmer temperatures may also explain selection of forest edges by squirrels. At ambient temperatures below 20°C red squirrels must increase their metabolic rate to maintain their body temperature (Irving *et al.* 1955). Ferron *et al.* (1986) found that squirrels increase feeding activity and stationary behaviours with decreasing air temperature. In this study, squirrels were in the sun most of the time when foraging in trees (71%-1996, 60%-1997). However, squirrels did not increase their sun exposure by foraging at edges (73%-1996, 57%-1997). Temperature measurements at the forest edge and interior, and more detailed observations on the response of squirrels to temperature changes, are needed to test this hypothesis.

Forest edges may provide abundant food and warmer temperatures but expose individuals to increased predation risk. Increased predation risk has been used to explain edge avoidance by small mammals (e.g., Bowers and Dooley 1993). I suggest that predation risk is low at a forest-pipeline edge. Although I did not directly test this hypothesis, survival patterns of squirrels at this site support this prediction. Northern goshawks (*Accipiter gentilis*), red-tailed hawks (*Buteo jamaicensis*), lynx (*Lynx canadensis*) and coyotes (*Canis latrans*) are the main predators of red squirrels in my study area (Stuart-Smith and Boutin 1995, Boutin

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unpubl. data). These predators may use the pipeline as a travel route (e.g., lynx, coyotes; O'Donoghue *et al.* 1998) or may benefit from increased prey visibility and capture success in a forest clearing (avian predators; Preston and Beane 1997, Squires and Reynolds 1997). However, the summer survival of the marked squirrels on edge territories was high ($\geq 90\%$) and slightly greater than previous reports of adult survival in this study area (49-85% Stuart-Smith and Boutin 1995). Moreover, Anderson (unpubl. data) has found no differences in survival of juvenile squirrels on territories with and without a forest-pipeline edge at this site.

Lateral spruce cover was higher at forest edges than in the forest interior. Foliage density may decrease avian predation risk either by providing squirrels with sufficient cover when foraging on edge trees or by physically restricting avian attacks. Willow shrubs and remnant log piles may similarly impede ground-based predation by mammalian predators. Predation risk may, however, be high outside of the forest canopy. Increased predation risk and absence of conifer foods could explain infrequent use of shrub and pipeline habitat by red squirrels. To test whether high cover at edges reduces predation risk, foliage and ground cover could be reduced. The survival of squirrels could then be compared among the altered edges and control sites.

**Individual vs. population level responses to fragmentation**

How small mammals respond to forest edges is usually examined at the population level using trapping data. Conclusions based on relative abundance, however, may differ from, and not necessarily reflect, the performance of individuals at edges (Van Horne 1983). For example, Bowers *et al.* (1996) found that meadow voles (*Microtus pennsylvanicus*) were less abundant in fragmented than continuous grassland. However, female voles at patch edges were larger, had larger home ranges, and reproduced more frequently than females in the patch interior. They argued that increased plant production outweighed any increase in predation risk at edges, and would explain the use of edges by the larger, dominant individuals. By studying the response of individuals at edges, they were able to provide mechanistic explanations for population patterns at a landscape level.

Selection of edge habitat by individual red squirrels is not necessarily expected based on population level studies in fragmented habitats. The density and home range size of European red squirrels (*Sciurus vulgaris*) are reduced in fragmented landscapes (Wauters *et*

*al.* 1994). European red squirrels also avoided clearcut, plantation, and young forest habitat in forest fragments (Andrén and Delin 1994). Bayne and Hobson (1998) found that the abundance of North American red squirrels and northern flying squirrels did not differ between the edge and interior of forest patches, though squirrels were more abundant in farm woodlots than in continuous or logged forest. Red squirrel densities were lower in thinned lodgepole pine (*Pinus contorta*) stands than in lightly thinned and unthinned stands in British Columbia (Sullivan and Moses 1986, Sullivan *et al.* 1996). However, the survival, recruitment and breeding parameters of the squirrels did not differ between these managed and unmanaged stands.

None of these studies, nor my own, have set out to compare the fitness of squirrels between forest edge and interior territories. Although I suggest that edges may be a profitable foraging location for squirrels, other factors such as patch size, isolation and conifer cover may be more important in determining the overall response of squirrels to fragmentation (e.g., Verboom and Van Apeldoorn 1990, Van Apeldoorn *et al.* 1994). In fact, increased bud abundance at edges could have little effect on the performance of squirrels on edge territories. Red squirrels have responded to supplemental feeding by reducing home range size, increasing the length of breeding seasons and producing second litters (Klenner and Krebs 1991). None of these parameters appear to be enhanced for squirrels at this forest edge. The average territory size of squirrels at edges (0.45 ha) is similar to previous reports for squirrels at this site (approx. 0.38 ha, Price *et al.* 1986). Squirrels produced only one litter in 1996 and 1997 (S. Boutin, unpubl. data.). Also, the percent of females breeding on edge territories (58%, n=17 for 1996; 54%, n=13 for 1997) was lower than the overall average for females on the study grids (66% for 1996, 80% for 1997; S. Boutin, unpubl. data).

**Conclusions**

I found that red squirrels selected for forest edge habitat in late spring and early summer. Edge selection is best explained by the response of squirrels to the seasonal abundance of white spruce vegetative buds at this forest edge. Warmer temperatures and a small increase in predation risk could also contribute to forest edge use at this site. Conifer buds are frequent in the spring and summer diet of red squirrels (Ferron *et al.* 1986, Wauters

*et al.* 1992). However, their relative importance likely depends on the abundance of more traditional foods (e.g., stored cones) in a given habitat or year.

Whether squirrels select edges for foraging in other landscapes likely depends on the age and type of forest edge. Squirrels may not select recent forest edges if conifer growth has not yet responded to increased light levels. The response of squirrels at a forest-pipeline edge may also differ from that at larger clearings. Further, squirrels in this and other northern forests, which are often naturally fragmented, may be preadapted to forest edges. Predators, predation risk and alternate foods vary among forested and agricultural landscapes and likely influence use of edges by squirrels (Sheperd and Swihart 1995, Bayne and Hobson 1998). Experimental manipulations of food abundance, forest cover and predation risk are necessary to test the mechanisms of edge selection I suggest here.

Finally, selection of a forest-pipeline edge does not necessarily imply that red squirrels will show a positive response to fragmentation. A reduction in cone abundance, conifer cover and forest area may decrease the fitness of squirrels in fragmented or managed landscapes. Future studies should focus on individual performance, rather than relative abundance, to determine how squirrels respond to forest fragmentation in a variety of landscapes. Researchers should compare the behaviour, reproduction and survival of individuals at edges to those in interior and continuous forest.

# CHAPTER 3. Experience increases the searching success of red squirrels for songbird nests.

## INTRODUCTION

Nest predation is the principal source of reproductive failure for birds (Ricklefs 1969, Martin 1992). Forest fragmentation and elevated rates of nest predation at forest edges (Paton 1994) are frequently blamed for declines in songbird populations (e.g., Robinson *et al.* 1995). Changes in predator diversity, abundance and activity at forest edges may all contribute to higher predation rates at forest edges. Few studies, however, have directly investigated habitat selection or nest searching behaviour by nest predators (but see Vickery *et al.* 1992). Most research has concentrated on describing predation patterns, rather than examining the mechanisms underlying predator behaviour.

In particular, there is debate over whether nest predators actively search for nests. Songbird nests are a short-lived resource; thus it is argued that developing search tactics for such a minor dietary component is not optimal (Angelstam 1986, Marini 1997). Rather, generalist predators are thought to encounter nests by chance during other foraging activities (Vickery *et al.* 1992, Norment 1993). According to this opportunistic hypothesis, the number of nests taken by a predator should increase as nest density increases, though the proportion of nests taken will remain constant or even decrease (e.g., Holling 1959, 1965). Alternatively, songbird nests may reach a density or profitability where predators alter their behaviour and actively search for nests. An increase in predation rates with increasing nest densities (Gates and Gysel 1978, Sugden and Beyersbergen 1986, Martin 1988) and in successive nest trials (Campbell 1995) suggests that an active response by an individual predator, or at least by a group of predators, does occur. Indeed, Gates and Gysel's (1978) "ecological trap" hypothesis is based on a functional response of predators to high nest densities at forest edges. Further, active search by nest predators, using nesting microhabitat search cues (Martin 1988, 1993) and area-restricted searching (Tinbergen *et al.* 1967), has been used to explain the choice of nesting microhabitat and inter-nest spacing of birds.

The opportunistic and active predation hypotheses make contrasting predictions on the relationship between nest survival and the number of nests a predator has previously taken. If a predator locates nests opportunistically, nest survival should be independent of prior nest-

finding experience by that predator. Rather, survival of nests should be related more to the habitat use and behaviour of an individual predator. For example, if a predator concentrates activity at the forest edge, nests should be found faster at forest edges. The active search hypothesis predicts an increase in searching success as a predator gains experience at finding nests. If area-restricted searching is used to locate successive nests, predator activity should increase near the nest site. If predators use nesting microhabitat as a search cue, predators should increase their searching intensity in other areas with the specific microhabitat cue.

Testing these hypotheses requires knowledge of how nests are situated in relation to the territory, home range or habitat use of individual predators. For most nest predators, behavioural observations are hindered by large territory size (e.g., corvids) or nocturnal activity (e.g., raccoons, deer mice, skunks; but see Vickery *et al.* 1992). Red squirrels are a common nest predator (Boag *et al.* 1984, Martin 1988, Darveau *et al.* 1997, Sieving and Willson 1998, Sloan *et al.* 1998), and are abundant in most conifer forests throughout North America (Banfield 1974, Nowak 1991). Individuals defend small territories (0.3-2 ha) year round (C. Smith 1968, 1981; Rusch and Reeder 1978; Gurnell 1984) and are active and easily observed during the day. Thus, red squirrels are ideal for studying nest predator searching behaviour.

To test the predictions of the active vs. opportunistic predation hypotheses, I conducted artificial nest experiments in combination with behavioural observations of red squirrels. Here I relate survival times of artificial nests to nest location, squirrel habitat use and prior nest-finding experience. My specific objectives were to (1) compare survival between nests on the forest edge vs. forest interior portion of a squirrel territory, (2) relate nest survival to territory use and behavioural characteristics of individual squirrels, (3) relate nest survival to prior nest-finding experience of squirrels, and (4) monitor microhabitat use by squirrels, using sand trackboards, at various spatial scales to determine if squirrels change activity patterns after nests are found to increase searching success.

## METHODS

### Study area

Research was conducted during August, 1996 and May to July, 1997 in white spruce forest near Kluane Lake, Yukon Territory. The same study areas were used as described in Chapter 2.

### Artificial nest design and protocol

Artificial nests containing one Japanese quail (*Coturnix japonica*) egg (2.3 x 3.0 cm) and one plasticine egg (2.0 x 3.8 cm) were used to test the influence of nest location and prior experience on nest survival. Dirt and clay were mixed with the plasticine when molding the eggs to mimic the mottled colour of the quail egg. In 1996, I constructed nests by hand using local grasses and mosses. Nests were approximately 10 cm wide and 5-7 cm deep. Wicker canary nests (11 cm wide, 7 cm deep) coated in mud and lined with moss were used in 1997. To reduce loss of nests and plasticine eggs to predators, I used wire to attach the plasticine eggs to the nests and to secure nests on the ground. Timers were used to record predation events in 1997. Timers consisted of a clock module soldered to a microswitch on which the quail egg was placed. When the quail egg was removed, and the microswitch arm depressed, the circuit within the clock module was opened and timing was stopped (for details see Ball *et al.* 1994, Bayne 1996). The timing devices were constructed using epoxy, black electrical tape, paper clips and solder. They were sealed in small plastic bags (5 x 6.5 cm) and attached to the wicker nests with wire. I camouflaged the timers by covering the clock module and wires with dried moss. To minimize human scent, I wore rubber gloves rubbed with spruce needles when constructing and handling nests and eggs. Eggs and nests were stored with spruce branches and leaf litter.

I used ground nests in all experiments. Several songbird (e.g., *Junco hyemalis*, *Wilsonia pusilla*, *Zonotrichia leucophrys*, *Vermivora celata*) and grouse (*Bonasa umbellus*, *Dendragapus canadensis*) species in the study area nest on the ground. Trial experiments in 1996 suggested that red squirrels were the primary predators of ground nests while grey jays (*Perisoreus canadensis*) were the main predators of nests in trees and shrubs (also see Yahner and Cypher 1987, Nour *et al.* 1993). These trials also suggested that grey jays could be the more efficient of the two predators, as the median survival time for nests on the ground was

over twice that for nests in trees or shrubs (Appendix 6). I attempted to mimic the natural nest sites of ground-nesting passerines in the area, particularly those of the dark-eyed junco (*Junco hyemalis*). Nests were placed within depressions dug under logs (1996), within grass tufts or hummocks (1996) or at the base of willows (1996 & 1997). Specific nest sites were chosen based on the amount of overhead grass or herbaceous cover to camouflage the nest and their contents. If overhead cover was particularly sparse, I used a small section of spruce or aspen bark to partially cover the nests to reduce nest detection by grey jays.

Nests were checked once (1997) or twice (1996) daily to record the time of predation and to identify predator species. I identified predators by examining damage to the nests, egg shell remains, and tooth and beak marks in plasticine eggs. I compared the remains of eggs and nests to those placed in live-traps with various small mammal and bird species found in the area (see Appendix 7). These individuals were trapped and censused during separate research on other study grids. I also compared tooth marks to plasticine impressions from museum skulls of potential predator species (Appendix 7). The size and shape of tooth and beak marks were used to categorize species within the avian and small mammal groups. Tracks in sand trackboards used in 1997 (see below), and the diurnal or nocturnal occurrence of predation also helped to identify predators. When checking nests, I minimized my disturbance of the surrounding vegetation and checked nests from as far away as possible (>1 m). Because I was interested in predation by red squirrels, nests were considered depredated only if the quail egg appeared to have been destroyed or removed by a red squirrel. If this requirement was not met, I recorded the disturbance and predator species, and replaced damaged or missing nests and their contents.

**Identification and behavioural sampling of red squirrels**

I identified squirrel territory owners and territory boundaries through live-trapping and behavioural observation of individual squirrels (see Chapter 2). Behaviour samples of red squirrels were collected as described in Chapter 2. I used trapping records from previous years (S. Boutin, unpubl. data.) to estimate the age of squirrels used in experiments in 1997. Trackboard activity (see below) was used as a measure of habitat use at smaller scales.

## Experimental design

*Effect of prior experience on nest survival between squirrels (1996)*

In August 1996, I tested the influence of prior nest-finding experience on the searching success of red squirrels by comparing nest survival times between squirrels that had or had not previously found a nest. Thirty squirrels were randomly assigned to 15 pairs. These squirrels were not required to have a forest edge within their territory. I placed a single nest on the midden of one squirrel in each pair; nothing was given to the second squirrel. Once the nest on the midden was depredated (i.e. the quail egg was removed or eaten) by the first squirrel, a second nest was placed 10-15 m away from the midden in both squirrel territories. I compared the time required for each squirrel to find the non-midden nests within each pair.

*Factors influencing squirrel searching success (1997)*

During May-July 1997, I tested the effect of nest location, prior experience and territory use on the searching success of red squirrels. I located 40 squirrel territories bordering a forest edge. I chose 5 willow bushes, each 8-10 m apart, as trackboard sites along the forest edge and forest interior border of each territory (Figure 3.1). I estimated previous activity by red squirrels at each willow by recording the number of cache holes, quantity of spruce cone bracts and distance to red squirrel runways.

Aluminum toaster oven trays (16 x 24 x 1.5 cm) sprayed with black paint and filled with sand were used as trackboards. Trackboards were set in small areas cleared of vegetation and leaf litter so that the sand was level with the ground surface. Two trackboards were set on either side of each of the 5 edge and 5 interior willows on each territory; each of the 40 squirrel territories therefore contained 20 trackboards. I checked trackboards daily and identified tracks to species by comparing the size, shape and pattern of tracks to those of known species (either naturally occurring or in trackboards during trial experiments) and by using descriptions in Murie (1954). Droppings, digging patterns, teeth marks, and food items found on the trackboards also aided in identifying species. I recorded the number of times each species appeared to cross the trackboard and percent coverage of the tracks. After recording activity, I cleared each trackboard of tracks and debris, refilled any lost sand and, if necessary, lightly sprayed the sand with water to minimize sand loss and track concealment by wind.

Forest Interior

N2   a   c   N1   b

opp n1   opp n2

Interior nest
treatment

Forest-Pipeline Edge

opp n2

midden

N1   c   b   N2   a

opp n1

Edge nest
treatment

1 red
squirrel
territory

willow

track
board
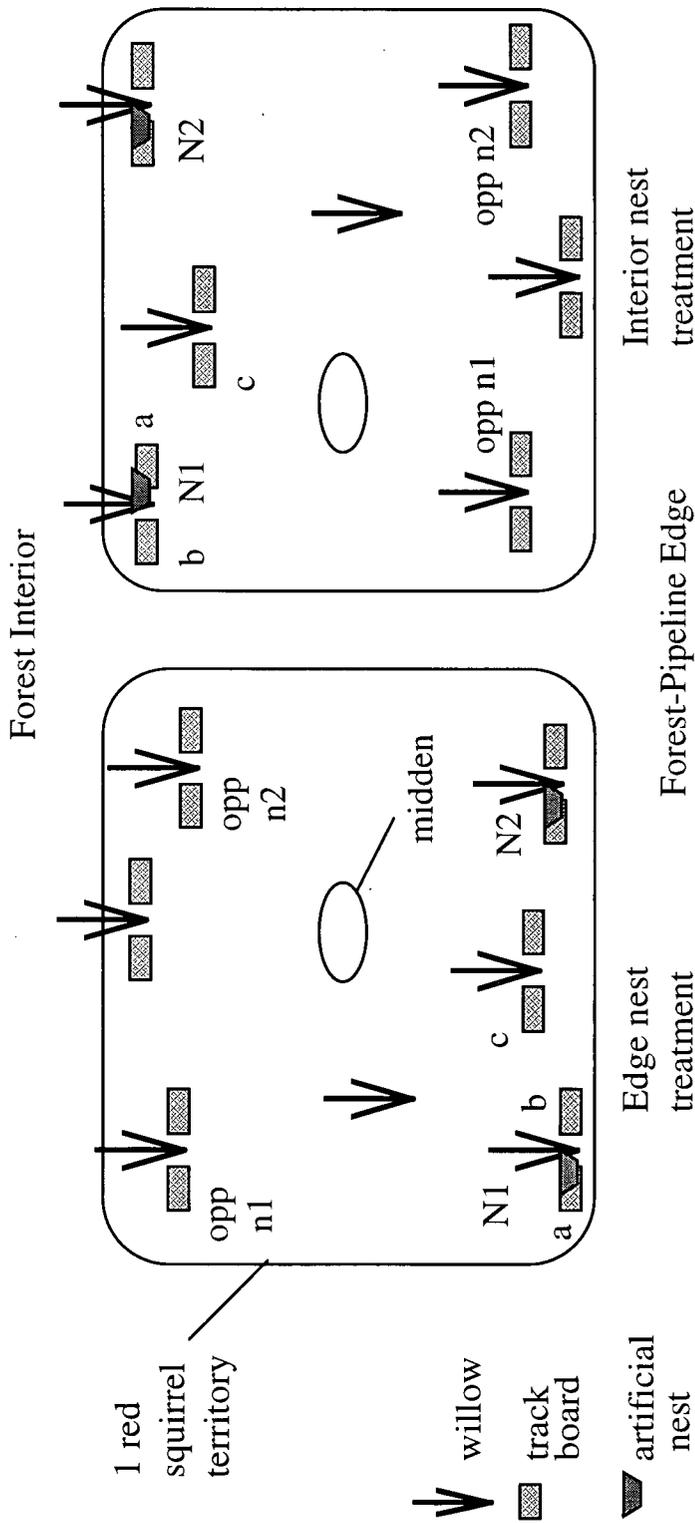
artificial
nest

**Figure 3.1.** Schematic of experimental design for the artificial nest experiment in 1997. Forty squirrel territories bordering the forest-pipeline edge were located and territory boundaries determined by observing territory owners. Two sand filled trackboards were placed at each of 5 willow shrubs at the forest edge and forest interior border of each territory (only 3 willows/territory border are shown above). After squirrel activity at trackboards had been monitored for at least 5 days, 1 artificial nest was placed at the base of 2 willows in each territory. Both nests were placed either at the forest edge (n=22) or forest interior (n=18) border in each territory. Nests were checked daily for at least 14 days or until nests had been depredated by a red squirrel. Trackboard activity was monitored for at least 5 days after the last nest had been depredated.
N1=1st nest depredated, N2=2nd nest depredated, a= nest site trackboard, b= nest willow trackboard, c= adjacent willow trackboard, opp n1= pair of nest site trackboard on opposite territory border, opp n2= pair of nest site trackboard on opposite territory border.

Although I was able to differentiate ground squirrel from red squirrel tracks in most cases (>85%), I may not have been able to distinguish between flying squirrel and red squirrel tracks. A large underestimate of flying squirrel activity, however, is highly unlikely. Northern flying squirrels are relatively rare at this study site (S. Boutin, pers. comm.), and less than 3.5% of all nest disturbances (n=226) occurred between midnight and 0500 hrs, when flying squirrels are most active.

After trackboard activity had been recorded for at least 5 days, I placed one nest at the base of 2 of the willow shrubs either at the forest edge (n=22) or interior border (n=18) of the squirrel's territory. My initial assignment of each squirrel to edge or interior nest treatments was random. However, I reassigned squirrels to treatments if more than two neighbouring squirrels received the same nest location treatment. One nest was placed at the willow site with the highest red squirrel trackboard activity (high activity nest) and the other at the willow with the lowest activity (low activity nest; Figure 3.1). Trackboards and nests were checked daily for activity and disturbance until the quail egg had been removed or consumed by a red squirrel or for a maximum of 14 days. I continued to monitor the trackboards for five days after both nests had been depredated by red squirrels.

**Analysis**

*Survival of Forest Edge vs. Interior Nests*

I used a forward-stepwise Cox proportional hazard regression to test for the effect of nest location (forest edge or interior of squirrel territories) on nest survival. Nest location, the date nests were set out, and distance from the nest to the squirrel midden were entered as covariates of nest survival. I used this method of survival analysis as it makes no assumptions about the distribution of survival times, and can account for both censored data (i.e. nests that survived the 14 day trial) and additional covariates (season and midden-nest distance) (Lee 1992).

*Influence of the behaviour, territory use and sex of squirrels on nest survival*

The opportunistic predation hypothesis predicts that nest survival should be related to the territory use and behavioural patterns of each squirrel. To test this prediction within squirrel territories, I compared survival of the high activity and low activity nests. To test this

prediction between squirrels, I used a forward-stepwise logistic regression of nest survival. Parameters included in the logistic model were: red squirrel trackboard activity (see below) before nests were set out at (1) the nest site trackboard (% of all recorded activity), (2) all trackboards along the territory border with the nests (% of all recorded activity), (3) all trackboards at both territory borders; the number of squirrel cache holes at the nest willow; sex of the squirrel; whether squirrels depredated nests in experiments in 1996; the date the nest was set out; and the distance of the nest to the squirrel midden. The latter two parameters were included to account for variation not controlled for in the experimental design.

A forward-stepwise Cox proportional hazard regression was used to test the relation between the behavioural characteristics of squirrels and nest survival. Only nests on territories where behavioural data were collected between May 10 - 31, 1997 (n=8) were used in the analysis. Four characteristics were entered into the model: 1) proportion of time spent active on the ground (non-midden locations), 2) proportion of time spent traveling, 3) territory size, and 4) ratio of 50% core area size to total territory size. Territory size was calculated as described in Chapter 2. The ratio of core area to territory size was based on 50% and 100% home range estimates using the minimum convex polygon method and the CALHOME computer program (Kie *et al.*, 1994). None of the behavioural parameters were significantly correlated (Spearman Rank Correlations; all p>0.05).

*Effect of prior experience on nest survival within squirrels*

If squirrels learn to search for nests, searching success should increase with experience. To test this hypothesis, I compared survival times of the first and second nest found in each territory. The data were log transformed (log(x +1)) prior to a two-factor ANOVA. The location of the nest (edge or interior) was entered as a between group factor and the order in which the nest was found (found first or second) was used as a repeated measure factor.

*Use of search cues and area-restricted searching*

If squirrels use the willow nest site as a search cue, an increase in squirrel activity at all willows should be seen after the first nest is depredated. If squirrels find the second nest by

area-restricted search, squirrel activity should increase at willows between the two nests. I used trackboard data to test these predictions. I compared the average number of times red squirrel tracks crossed a trackboard per day five days before nests were set out and five days after nests were depredated (hereafter "activity"). Activity on trackboards for squirrels that failed to find nests within the 14 days was used as a temporal control. For these squirrels, I used trackboard activity 5 days after nests were set out as the "after predation" measurement. The five days excluded any days where tracks were obscured by rain.

I tested for changes in activity at 4 spatial scales: 1) the trackboard directly in front of the nest (nest site), 2) the trackboard on the opposite side of the willow from the nest (nest willow), 3) the trackboard placed at the adjacent willow, and 4) all trackboards at both the edge and interior territory borders (Figure 3.1). An increase in trackboard activity after the first nest is found is predicted at all spatial scales (i.e. all willows) if squirrels use nest microhabitat (i.e. willow) as a search cue. The area-restricted search hypothesis predicts an increase in activity only at the first three levels (nest site, nest willow and adjacent willow).

A log transform failed to normalize distributions for activity data at the nest site, nest willow and adjacent willow trackboards. I therefore used nonparametric tests to test for changes in activity at these scales. I first pooled edge and interior nest treatments after testing for differences between the two locations (Mann Whitney U tests, all p>0.05). I calculated changes in trackboard activity by subtracting activity before nests were set out from activity recorded after nests were depredated. Activity changes at the nest site, nest willow and adjacent willow were then compared between squirrels that did and did not depredate nests on their territory.

I tested for changes in squirrel activity at all trackboards at the forest edge and interior territory borders using a four-way ANOVA on the log transformed data. Nest site trackboards and the corresponding pair at the opposite territory border were not included when calculating activity at the territory borders (Figure 3.1). Nest location (edge vs. interior) and whether squirrels depredated nests were used as between group factors; the location of trackboards (edge vs. interior territory border) and time (before vs. after "predation") were used as repeated measures factors. Specifically, I was interested in: 1) whether squirrels changed their activity after nests were found (nest depredated x time factor),

and 2) whether changes in squirrel activity were confined to the territory border where squirrels encountered nests (nest location x trackboard location x time factor).

I used individual squirrels as my sampling unit in all of the above analyses. Two measures of nest survival were used depending on the factor being investigated (Table 3.1). For most analyses, I used time to first nest disturbance by a red squirrel as my dependent variable. For the 1997 experiment however, I wanted to ensure that squirrels received a "reward" or reinforcement after finding a nest. I therefore considered a nest to be depredated only if the quail egg was destroyed, consumed or removed by a red squirrel. Similarly, I used removal of the quail egg as a criterion for categorizing post-predation activity at trackboards. In most cases these two survival times were identical, as squirrels removed the quail egg during the first nest disturbance (see results). Most statistical analyses were performed using Statistica© (Statsoft 1995). I used SPSS© (SPSS 1995) for regression analyses.

## RESULTS

### General patterns of nest survival (1997)

At least one of the two nests on each squirrel territory was disturbed during the 14 day period. Red squirrels tended to discover the nests before other species (Table 3.2). Avian disturbance, primarily by grey jays, was half as frequent as that by red squirrels. Time to the first disturbance event within a nest pair, regardless of predator species, ranged from 0.02-12.53 days with a median of 1.95 days.

### Predation by red squirrels

Thirty of the 40 squirrels (75%) found and disturbed at least one of the two artificial nests on their territory within 14 days. Median time to the first disturbance by a red squirrel was 2.71 days (range = 0.02-10.36 days). Of the 30 squirrels finding the nests, 24 removed or destroyed the quail egg. In 19 of these 24 cases, squirrels took the quail egg during the first nest disturbance (median time to predation = 2.96 days, range = 0.02-10.95 days).

### Survival of edge vs. interior nests

Fourteen of the 22 squirrels with edge nests (64%) and 16 of the 18 squirrels with interior nests (89%) found nests during the 14 day trial. Location of nests on the forest edge

**Table 3.1**. Measures of nest survival used as dependent variables when analysing red squirrel predation on artificial nests.

| Factor Investigated | Dependent Variable |
| --- | --- |
| Edge vs. interior nest location | Time to $1^{st}$ nest disturbance by a red squirrel |
| Prior experience (between squirrels) | Time to $1^{st}$ nest disturbance by a red squirrel |
| Prior experience (within squirrels) | Time to $1^{st}$ quail egg predation by a red squirrel vs. elapsed time to disturbance by a red squirrel on the $2^{nd}$ nest |
| Characteristics of individual squirrels | Time to $1^{st}$ nest disturbance by a red squirrel |

**Table 3.2.** Percentage of first nest disturbance events within a squirrel territory (n=40) attributed to each nest predator. High and low activity refer to the amount of red squirrel activity recorded at nest site trackboards before nests were set out. Results are also presented using data from only the first of the two nests disturbed on each squirrel territory.

| Predator Spp. | High Activity Nests | Low Activity Nests | 1st Nest Found |
|---|---|---|---|
| Red Squirrel | 40 | 50 | 57.5 |
| Grey Jay & Avian Spp. | 30 | 22.5 | 22.5 |
| Ground Squirrel | 0 | 2.5 | 0 |
| Unknown | 25 | 17.5 | 20 |
| Not Disturbed | 5 | 7.5 | 0 |

or interior of a squirrel territory explained little variation in the length of nest survival (Table 3.3). The additional date covariate and midden-to-nest distance covariate did not significantly improve the model. Neither date (Mann-Whitney U test, $Z=1.71$, $p=0.09$), nor midden- nest distance ($T=-0.73$, $p=0.47$) differed between edge and interior nest locations. Removing these covariates and comparing Kaplan-Meier survival curves for edge and interior nests also revealed no difference in survival between edge and interior locations (logrank test, $X^2 = 1.05$, $p=0.29$).

**Effect of prior experience on nest survival**

*Between squirrel comparison*: Results from 1996 show that squirrels that had depredated a nest within the past 48 hours found a second nest 5.6 times (5 days) faster than squirrels without any prior experience with finding nests (Figure 3.2; Wilcoxon Matched Pairs test $Z=2.33$, $N=15$, $p=0.02$).

*Within squirrel comparison*: Although only 24 of 40 (60%) squirrels found and depredated nests on their territory in 1997, in all 24 cases both nests were taken within the 14 days. There were no cases in which squirrels failed to find the second nest after depredating the first.

Squirrels again found the second nest over 5 times faster than the first nest (Figure 3.3; two-factor ANOVA, "order found" term $F_{1,22}=10.24$, $p=0.004$). There was no significant effect of nest location (forest edge or interior) on time to predation (nest location $F_{1,22}=0.002$, $p=0.96$), nor was there a significant interaction between nest location and nest number (interaction $F_{1,22}=0.003$, $p=0.96$). I initially analysed the data using ANCOVA to test for the significance of the date on which nests were set out and midden-nest distance as covariates. As neither covariate was closely related to nest survival (all $p>0.05$), I did not use the covariates in the final ANOVA.

**Influence of territory use, behaviour and sex of squirrels on nest survival**

When setting out nests on each squirrel territory, I placed one nest at the trackboard and willow with the highest amount of activity by red squirrels and the other at the willow with the lowest activity. High activity sites had an average of $0.20 \pm 0.04$ ($\pm 1SE$) red squirrel visits/day (calculated over 5 days) while low activity sites had only $0.07 \pm 0.02$ visits per day

**Table 3.3.** Results of a Cox proportional hazard regression for the influence of nest location (edge or interior of squirrel territory), date nest was set out, and distance from nest to squirrel midden on nest survival times. Nest survival was calculated as the time to first nest disturbance by a red squirrel. None of the covariates provided sufficient information to be included in the forward-stepwise model (N=40).

| Parameter | $B^a$ | $Wald^b$ | df | p |
|---|---|---|---|---|
| Nest Location | -0.38 | 1.09 | 1 | 0.30 |
| Julian Date | -0.02 | 1.91 | 1 | 0.17 |
| Midden-Nest Distance | -0.01 | 0.21 | 1 | 0.65 |

[a] positive $B$'s (regression coefficient) indicate an increase in predation as the parameter increases, and from interior to edge for nest location.
[b] Wald test statistic for $H_o$: $B = 0$
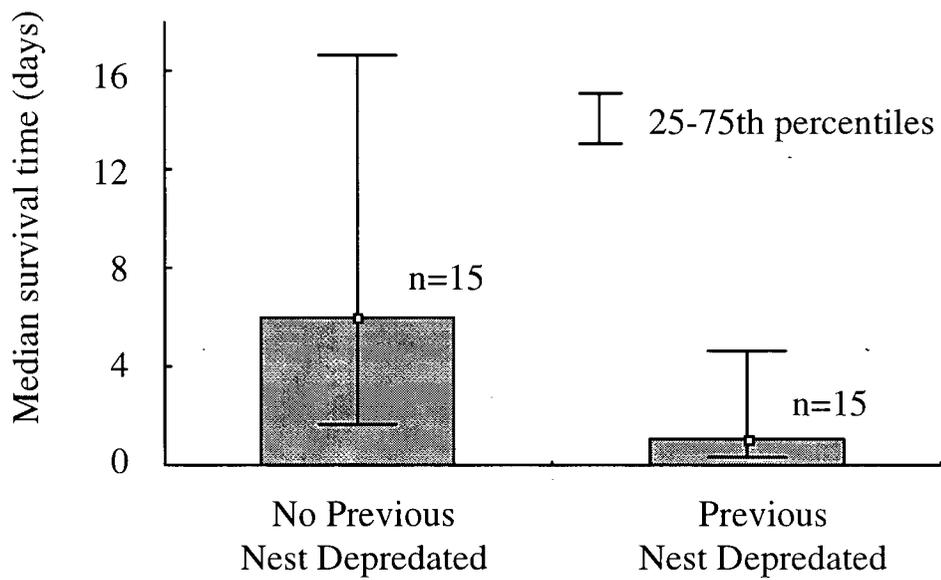
**Figure 3.2.** Comparison of median survival times of nests on squirrels territories where territory owners had or had not previously depredated an artificial nest. Nest survival was calculated as the time to first disturbance by a red squirrel.
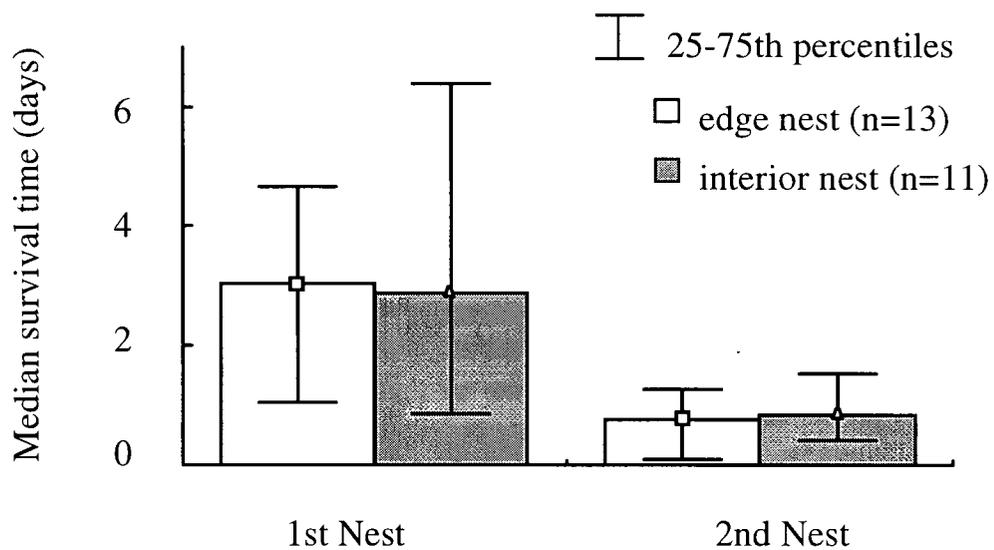
**Figure 3.3.** Comparison of nest survival between the first and second found nest on each squirrel territory (n=24). Survival of the first nest was calculated using time to first quail egg removal by a red squirrel. Survival of the second nest was calculated as the time between predation of the first nest by a red squirrel and subsequent disturbance of the second nest by a red squirrel.

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(Wilcoxon Matched Pairs test, Z=3.35, N=40, p<0.001). I found no relation between initial nest placement at high or low activity sites and the order in which nests were disturbed by squirrels; 15/40 high activity and 15/40 low activity nests were found first; 10 squirrels failed to find either nest. Comparing initial trackboard activity between the first and second found nest within each territory also showed no differences in initial activity between the first (0.17 ± 0.05 visits/day) and second (0.31 ± 0.06 visits/day) found nest (Wilcoxon Matched Pairs test, Z=1.60, N=30, p=0.11).

Step-wise logistic regression analysis revealed that experience at finding nests the previous year, date nests were set out and the number of cache holes at the nest willow were the only parameters that explained variation in nest survival among squirrel territories (Table 3.4). Nests were more likely to be depredated if the same squirrel had found nests during experiments in 1996, when nests were set out earlier in the summer, and as the number of cache holes near the nest decreased. Twenty-two of the 40 squirrels used in 1997 were studied in artificial nests experiments in 1996, 19 of which depredated nests in that year. Sixteen (84%) of these squirrels also successfully depredated nests during the experiment in 1997 compared to 8 (38%) of the 21 naïve squirrels.

Nest site activity is a subset of activity at the territory border and was correlated with this variable (Spearman R=0.48, p=0.002) as well as with midden-nest distance (R=-0.35, p=0.03). Because correlated variables violate assumptions of regression analysis (Zar 1984), I repeated the above analysis without the territory border activity and midden-nest distance variables and again without the nest site activity variable. These analyses did not change the overall results; experience in 1996, the date the nest was set out and the number of cache holes were the only variables included in both of the final models.

There was a strong interrelation between experience from 1996 experiments and squirrel age. Experienced squirrels were significantly older (mean age ± 1SE = 2.74 ± 0.23 years, n=19) than inexperienced individuals (1.14 ± 0.14 years, n=21; Mann Whitney U test Z=4.77, p<0.001). When entered in place of experience in 1996, squirrel age significantly contributed to the logistic model. To distinguish between age and experience effects, and to further examine factors influencing nest survival within the experienced and naïve squirrels, I performed separate Cox regression analyses of survival for nests on territories of experienced

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**Table 3.4.** Results of a forward step-wise logistic regression for factors significantly contributing to the model of nest survival on squirrel territories. Experience in 1996 refers to whether squirrels depredated a nest during experiments in 1996. Date nests were set out on each territory and number of squirrel cache holes at the base of the willow with the nest were also included in the model (N=40).

| Parameter | Model Improvement | |
| --- | --- | --- |
| | Change in X2 | p |
| **Included in the final model** | | |
| experience in 1996 | 9.36 | 0.002 |
| date | 4.16 | 0.042 |
| number of cache holes | 4.19 | 0.041 |
| **Not included in the final model** | | |
| nest site activity | | |
| territory border activity | | |
| total trackboard activity | | |
| sex of the squirrel | | |
| midden-nest distance | | |

and naïve squirrels. Variables tested in each model were the age and sex of the squirrel, percent activity at the nest site, overall trackboard activity, number of nest willow cache holes, and the date nests were set out. Age did not significantly contribute to the survival model for either the experienced or naïve squirrels. For naïve squirrels, only the sex of the territory owner was included in the final model ($X^2=5.94$, df=2, p=0.039). Nest survival was lower on female than male territories. None of the variables contributed to the model of nest survival for experienced squirrels. Therefore, experience, not age, is the dominant factor influencing whether squirrels find a nest.

Behavioural characteristics of individual squirrels explained little variation in nest survival among territories (Table 3.5). None of the behavioural covariates contributed significantly to the model of nest survival. However, squirrels that used a greater portion of their territory (i.e. a high ratio of 50% core area-to-territory size) tended to find nests faster than squirrels that concentrated activity in a smaller portion of their territory. Behavioural data were available for only 8 animals and all but one of these individuals found nests on their territory.

**Use of nest site search cues and area-restricted searching**

*Changes in trackboard activity at the nest site, nest willow and adjacent willow*

For squirrels that depredated nests, trackboard activity at the nest site doubled after the first nest was depredated (Figure 3.4; Wilcoxon Matched Pairs Z=2.90, N=24, p=0.004). Activity also increased at the trackboard opposite the nest but at the base of the same willow (Z=2.05, N=24, p=0.04). There was no change in squirrel activity at willows adjacent to the nest willow (Z=0.08, N=24, p=0.94).

Squirrels that had nests on their territory but did not remove or consume the quail egg did not show similar increases in trackboard activity at the nest site or nest willow level (Table 3.6, Figure 3.4). There was no difference in activity change at the adjacent willow between squirrels that did or did not depredate nests; both groups showed little change in activity at this level.

**Table 3.5.** Cox proportional hazard regression results for the influence of squirrel behaviour on nest survival times. Nest survival was calculated as the time to first nest disturbance by a red squirrel. None of the covariates provided sufficient information to be included in the forward-stepwise model (n=8).

| Parameter | $B^a$ | $Wald^b$ | df | p |
|---|---|---|---|---|
| ground activity | 0.04 | 0.37 | 1 | 0.54 |
| traveling activity | 0.00 | 0.00 | 1 | 0.98 |
| territory size | 0.00 | 0.20 | 1 | 0.65 |
| 50% core area:territory size | 7.84 | 3.45 | 1 | 0.06 |

[a] positive $B$'s (regression coefficient) indicate an increase in predation as the parameter increases

[b] Wald test statistic testing $H_o$: $B = 0$

**Figure 3.4.** Comparison of squirrel trackboard activity before nests were set out and after the first nest "predation" for squirrels that did and did not depredate nests on their territory. Changes in trackboard activity are shown for trackboards at increasing distances from the nest site: a) nest site (trackboard directly in front of the nest), b) nest willow (trackboard at the base of the same willow as the nest but at the opposite side), c) adjacent willow (trackboard at an adjacent willow without a nest). * p<0.05 (Wilcoxon Matched Pairs test).
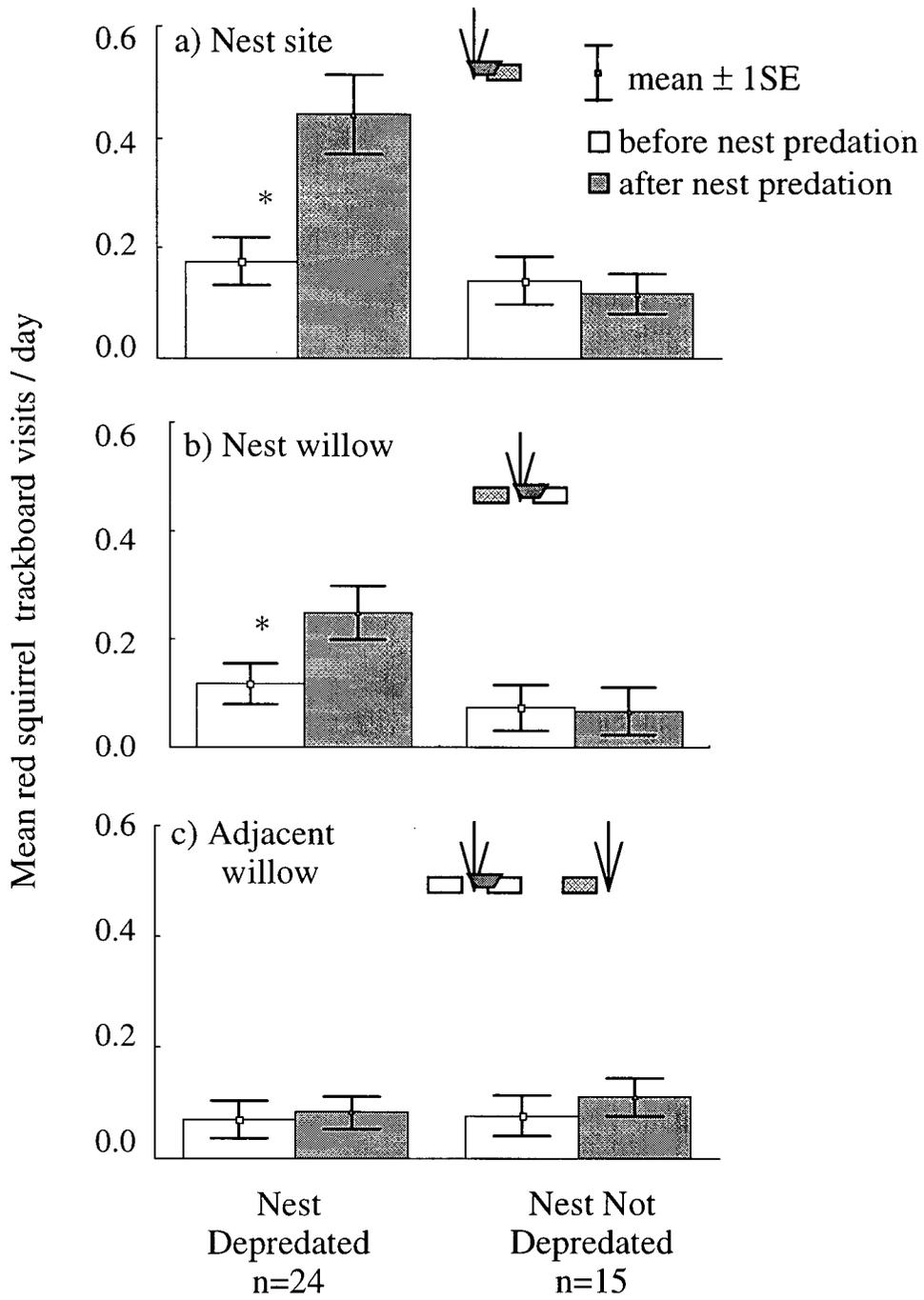
**Table 3.6.** Comparison of changes in red squirrel trackboard activity after nest "predation" between squirrels that did or did not depredate artificial nests on their territory. Activity change was calculated by subtracting trackboard activity before nests were set out from activity recorded after nests were depredated. Results are presented for trackboards directly in front of the nest (nest site), opposite the nest but at the base of the same willow (nest willow) and at an adjacent willow without a nest (adjacent willow).

| Trackboard Location | Activity Change-Nest Depredated (n=24) Mean ± 1SE | Activity Change-Nest Not Depredated (n=15) Mean ± 1SE | Mann-Whitney U Results | |
|---|---|---|---|---|
| | | | Z | p |
| Nest site | 0.27 ± 0.08 | -0.02 ± 0.07 | 2.68 | 0.008 |
| Nest willow | 0.13 ± 0.07 | -0.01 ± 0.06 | 2.12 | 0.033 |
| Adjacent Willow | 0.02 ± 0.05 | 0.03 ± 0.06 | -0.49 | 0.627 |

*Changes in overall trackboard activity at forest edge and interior territory borders*

Overall, squirrel activity was higher at forest edge than forest interior trackboards (Figure 3.5; 4-way ANOVA, trackboard location factor $F_{1,35}=13.57$, $p<0.001$). There was a general increase in activity at all trackboards after nests were depredated (time $F_{1,35}=7.25$, $p=0.01$). This increase was most pronounced for squirrels receiving edge nest treatments (time x nest location $F_{1,35}=4.66$, $p=0.04$). However, trackboard activity and activity change did not differ between squirrels that did or did not depredate nests (nest depredated factor and all interactions $p>0.05$). Change in trackboard activity also did not differ between edge and interior trackboards on a squirrel territory (time x trackboard location $F_{1,35}=0.01$, $p=0.90$), even when location of the nest was considered (time x trackboard location x nest location $F_{1,35}=3.83$, $p=0.06$). The only statistically significant increase in activity was for interior trackboards on squirrel territories where edge nests were depredated (Tukey's test for unequal sample sizes (Spjotvoll and Stoline test), $p=0.04$).

## DISCUSSION

My results support predictions of the active search hypothesis for red squirrel predation on the contents of artificial nests. Only 24 of 40 squirrels depredated nests within their territory, but in all 24 cases both nests on the territory were taken. Contrary to the opportunistic predation hypothesis, nest survival was not explained by squirrel activity at the nest site, nor by larger scale microhabitat use or behavioural variables. Squirrels that had depredated artificial nests the previous year and squirrels receiving nests earlier in the summer were more likely to depredate nests on their territory. I found no evidence for an "edge effect" on nest predation; nest survival did not differ between forest edge and forest interior locations of squirrel territories. Red squirrels learned to search for nests in that nest survival times decreased as squirrels gained experience at finding nests. Squirrel activity at the willow nest site doubled after nests were found, however, I found no consistent change in activity at non-nest willows or at larger spatial scales. Though squirrels may increase their search intensity at the nest willow, the scale of the search is not large enough explain how successive nests are found. Therefore, neither the use of nest site search cues nor area-restricted
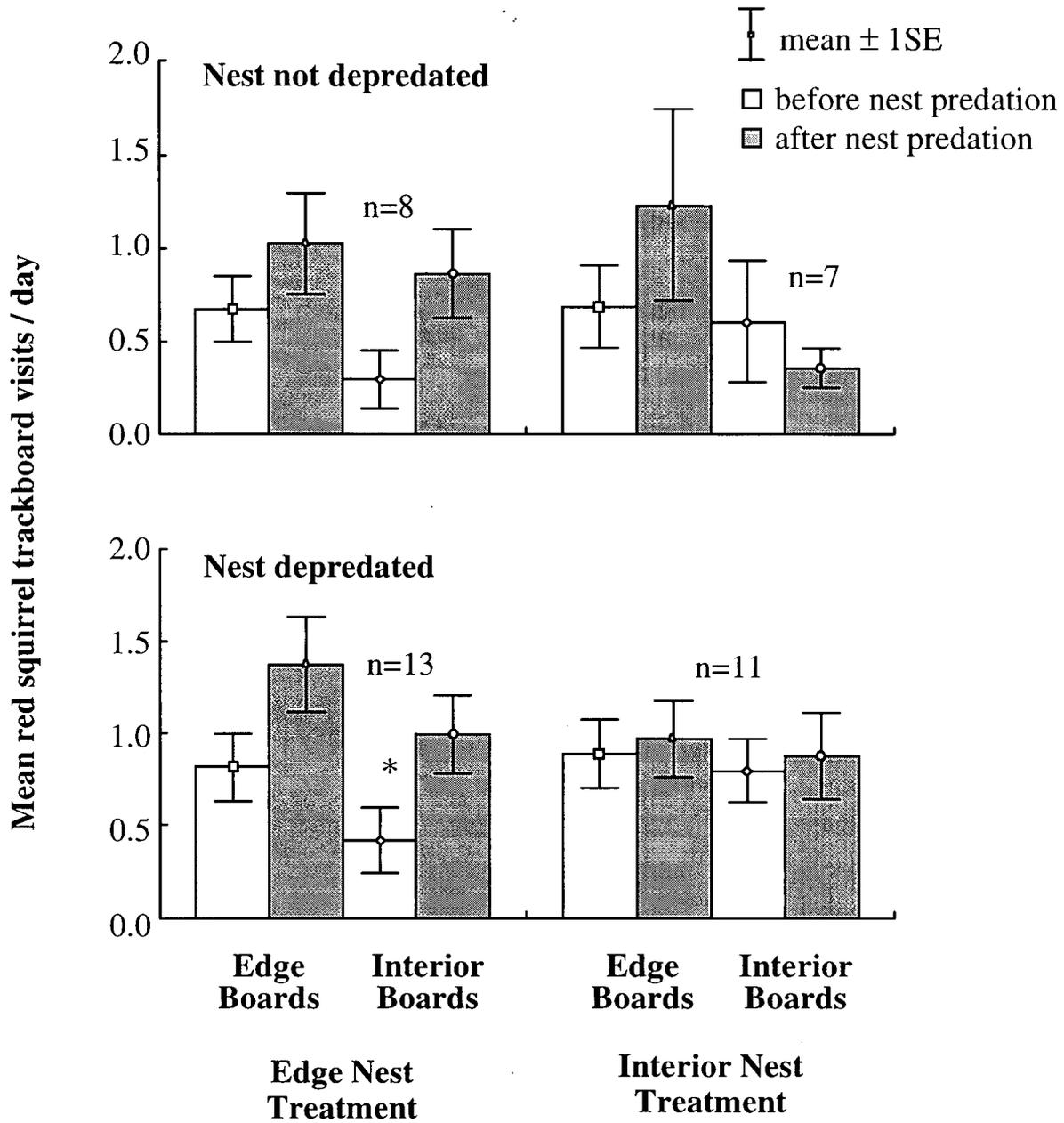
**Figure 3.5.** Comparison of squirrel activity at all forest edge and forest interior trackboards before nests were set out and after the first nest "predation". Trackboard activity is shown separately for squirrels that did and did not depredate nests and, within each graph, for squirrels receiving nests either on the forest edge or forest interior of their territory.

\* $p < 0.05$ (Tukey's post hoc test for unequal sample sizes)

searching appear to fully explain how squirrels learned to find nests. Instead, squirrels seem to increase their searching success by using the nests, or nest contents, themselves as a search image.

## Survival of edge vs. interior nests

The majority of studies that have tested the effect of forest edge on nest survival have found elevated predation rates at forest edges (Paton 1994), though this conclusion may be habitat specific (Andrén 1995). Most studies have been conducted in agricultural or otherwise developed landscapes (see Andrén 1995). In many of these areas, anthropogenic food sources (e.g., crops, refuse) support an abundant and diverse community of generalist predators (e.g., crows, ravens, mice, raccoons, but see Hannon and Cotterill 1998). There is less evidence for an "edge effect" in forested landscapes (e.g., Rudnicky and Hunter 1993, Hanski *et al.* 1996) where predators are typically resident forest species (e.g., gray jays, red squirrels). Studies at forest edges in western Canada have identified red squirrels as a primary nest predator and found no differences in predation rates between forest edge and interior locations (Campbell 1995, Cotterill 1996, Bayne and Hobson 1997a; but see Boag *et al.* 1984).

My results at this forest-pipeline edge support previous work on edge effects for predation on artificial nests by red squirrels. However, my definition of forest edge and interior differs from that used by others. In most studies, interior nests are placed on transects that are 50 - >1000 m from forest edge transects (Paton 1994). Depending on the home range of a nest predator, the same or different individuals may be depredating edge and interior nests. For red squirrels, with territories sizes generally less than 2 ha (Rusch and Reeder 1978), edge and interior nests would be located on the territories of different individuals. I defined forest edge and interior at the scale of an individual squirrel and did not compare predatory ability between squirrels on territories with and without forest edges. As previous studies have not found an edge effect for red squirrel predation on nests (e.g., Cotterill 1996, Bayne and Hobson 1997a), a difference in searching efficiency between squirrels at edges and in interior forest seems unlikely, at least with respect to artificial nests.

**Variation in searching success among red squirrels**

After depredating a nest, red squirrels quickly located other nests on their territory. However, not all squirrels found the first nest. From the opportunistic predation hypothesis, squirrels should have had a greater chance of finding nests in frequently used areas. I found no evidence of this pattern in my study. Survival of nests among and within squirrel territories was not explained by squirrel activity on trackboards at the nest site, at the territory border with the nest, or at willow bushes in general. Behavioural characteristics of individual squirrels also did not explain variation in nest survival. Further, a decrease in predation on ground nests later in the season was negatively correlated with increased foraging on the ground by squirrels in mid to late summer (Chapter 2). The only measure of squirrel activity that contributed to the nest survival model, number of cache holes, was positively correlated with nest survival.

My results contradict previous studies that have suggested a strong relation between nest survival and predator activity. Vickery *et al.* (1992) found that predation rates were positively correlated with the activity of skunks on study grids, and suggested that skunks inadvertently locate nests while foraging for invertebrates. Similarly, ground squirrels were thought to incidentally depredate nests while using (With 1994) or avoiding (Norment 1993) shrub cover. I would not predict a correlation between predator activity and nest survival if the behaviour of predators is random. Benhamou (1996) suggested that red squirrels randomly forage for scattered caches in spring and summer when cone stores are low. This random search hypothesis would explain the lack of correlation between squirrel activity and nest survival. It is also consistent with the trend for lower nest survival on territories where squirrels used a greater portion of their territory. I was able to improve on previous studies by determining the identity, habitat use, and experience level of individual predators. Still, trackboard counts are an indirect measure of activity, and I could not determine the exact activity a squirrel was engaged in immediately prior to locating a nest. Determining the context in which a predator locates a nest is necessary to fully test the opportunistic predation hypothesis.

## Learning by nest predators

I have shown that red squirrels learn to search for nests. I found that squirrels found nests over five times faster after depredating a single nest. Moreover, this increase in searching efficiency was retained for at least a year after the predation event. To my knowledge, this is the first study to test whether individual predators learn to search for nests, though this ability has been implied in numerous studies (e.g., Tinbergen 1967; Martin 1988, 1993). Increased search efficiency by individual predators could explain the lack of independence of predation events among neighbouring nests (Martin 1988, Cotterill 1996, Bayne and Hobson 1997b) or variation among study areas (Reitsma *et al.* 1990, Campbell 1995, Marini 1997). Similarly, Stefan 1998) suggested that individual red squirrels learned to prey on juvenile snowshoe hares to explain why survival among snowshoe hare littermates was correlated.

Learning is thought to be most common in species with specialized or constant diets (e.g., hummingbirds, honeybees; Bell 1991). Developing and retaining search skills for rare food items, such as songbird nests, is not considered optimal for species with broad diets (Bell 1991). Songbird densities are low at my study site (1.69 males/ha, Folkard and Smith 1995) and squirrel territories would thus contain only 1-2 songbird nests each year. In this context, the observed learning ability of squirrels might seem surprising. However, the ability to learn novel foraging tasks rapidly is characteristic of many generalist predators (e.g., badgers, Mellgren and Roper 1986; coyotes, Bekoff 1978; corvids, Savage 1995).

I suspect that predation on nests by red squirrels depends on the relative value and abundance of traditional food sources. It may be "optimal" for squirrels to learn to search for alternate foods early in the season when cone stores are low and reproductive energy demands are high. High energy requirements for lactating females (Humphries and Boutin 1996) could contribute to lower nest survival on territories of naïve female squirrels. Callahan (1993) suggested that the high calcium and protein content of vertebrate prey, including eggs, may explain carnivory in squirrels. This modified optimality argument could explain the increase in nest survival later in summer. In mid to late summer squirrels devoted most of their time to harvesting and caching food items for the winter (Chapter 2). In fact, I attributed the failure

of squirrels to depredate nests in a separate experiment in August 1997 to a large mushroom crop that year (S. Boutin, P. Carrier, unpubl. data).

**Search mechanisms: search cues and area-restricted searching**

Predators are thought to learn to search for cryptic prey by forming search images for the prey themselves or another associated visual cue (e.g., Tinbergen 1960, Peitrewicz and Kamil 1979). Alternatively, Guilford and Dawkins 1987 (also see Gendron and Staddon 1983) suggested that a decrease in search rate after prey is found better explains the increase in search efficiency. If predators slow their search and focus on a limited area (i.e. area-restricted search; e.g., Smith 1974, Benhamou 1994) they may be better able to perceive and process visual information (Guilford and Dawkins 1987). Both the search image and area-restricted search hypotheses could explain how nest predators learn to search for nests. Because the latter hypothesis does not require focusing on a single prey type (Guilford and Dawkins 1987, Bell 1991), it may better explain why nest predators learn to search for rare nest prey.

My results suggest that nest microhabitat was not used as a search image by red squirrels. Martin (1988, 1993; also see Skutch 1985) proposed that variation in nesting microhabitat among coexisting songbird species has evolved in response to predators using nest microhabitats as a search cue ("diversity/predation hypothesis", Ricklefs 1989). If squirrels used this search cue (i.e. willow), I should have seen increased, rather than constant, squirrel activity at non-nest willows after the first nest was depredated. Several studies have tested the effect of unique nest microhabitat on nest survival using natural (Martin 1988, Hoi and Winkler 1994) and artificial (Marini 1997, Hochachka unpubl. data) songbird nests. The results of these studies are equivocal, with evidence both for (Marini 1997, Martin 1988) and against (Hoi and Winkler 1994, Hochachka unpubl. data) the search cue hypothesis.

Area-restricted search also cannot explain how red squirrels located successive nests. Nests were an average of 19.3 m apart and over half of the squirrels (13/24) found the second nest within a day of depredating the first. Squirrels doubled their activity at the nest willow after finding the first nest. However, this increase did not extend to spatial scales large enough (i.e. adjacent willows) to explain how the second nest was found. Area-restricted searching by nest predators is thought to explain the distancing of nests between and within

avian species (e.g., Tinbergen *et al.* 1967). Studies testing this hypothesis, however, have found no consistent relation between inter-nest distance and predation rate (review by Andrén 1991; Schieck and Hannon 1993; Hochachka unpubl. data). Area-restricted searching may be adaptive in red squirrels in that several commonly-used foods have a patchy distribution in squirrel territories (e.g., cones or buds on productive trees, fungi). Squirrels are known to increase their search effort in the immediate vicinity of a found food item (pers. obs., Benhamou 1996). Though it could be useful for finding common food items, intensifying search at this small scale would be of little use to squirrels searching for natural nests at low densities.

The fact that red squirrels continued to return to the nest site after the nest had been removed suggests the use of spatial memory (Benhamou 1994). Spatial memory is an obvious advantage for food storing species such as red squirrels, though it is thought to be most common in birds (e.g., Shettleworth and Krebs 1982, Vander Wall 1989). Mammals are thought to rely more on olfactory cues to recover cached items (e.g., Vander Wall 1989). More recent evidence suggests that sciurids use spatial memory (Jacobs and Liman 1991, Devenport and Devenport 1994) and/or visual landmarks (Vander Wall 1991, Macdonald 1997) to return to profitable foraging patches or cache sites. Spatial memory, in combination with area-restricted searching, may be used by red squirrels to relocate productive patches or cache sites (Benhamou 1994, 1996). Again, how or if such search mechanisms are used to locate items in unknown locations, such as songbird nests, is uncertain.

Squirrels found nests in a variety of non-willow locations in 1996, yet this experience had a strong effect on their searching success in 1997. This further suggests that squirrels use mechanisms other than area-restricted search and nest site search cues to locate nests. It is possible that squirrels improved their ability to recognize nests by using the nest or eggs as a search image (Tinbergen 1960). Also, these search "images" may have been olfactory rather than visual (Nams 1991). Whelan *et al.* (1994) and Clark and Wobeser (1997) have shown that artificial nests given scent treatments have poorer survival than unscented nests. Nams (1991, 1997) has shown that skunks use olfactory cues to increase their abiltity to detect foods, including eggs, over time. Squirrels appear to use scent to differentiate between

species of spruce cones (Brink and Dean 1966) and to locate underground fungi (pers. obs.). Thus, it is reasonable to suggest that squirrels use olfactory cues to locate nests.

**Conclusions**

Red squirrels clearly are able to learn to search for artificial nests. Surprisingly, measures of squirrel activity had no influence on whether an individual would find a nest in the first place. I could not determine from my results how squirrels located nests. Squirrels may initially detect nests during random searching bouts when traditional food sources are limited (Benhamou 1996). Neither area-restricted search nor microhabitat search cues can explain how squirrels were able to efficiently locate the second nest on their territory. Learning is best explained by squirrels using the nest itself, or associated scents, as a search image. Video cameras would be useful in future studies to determine if squirrels find nests during other activities and if squirrels change their behaviour after nests are found. To test the use of olfactory cues, squirrels could be conditioned to artificially scented nests and the survival times of scented and non-scented nest compared (see Clark and Wobeser 1997).

The principal result from this study is that red squirrels quickly learned to find artificial nests. Squirrels should have a greater chance of finding a nest, and becoming efficient predators, as the number of nests within their territory increases. Stefan (1998) has shown that red squirrels exhibit a functional response to increasing juvenile hare densities. The nesting density of songbirds can be higher at forest edges than in the interior forest (Gates and Gysel 1978, Hansson 1983) and bird abundance may initially increase in recent forest fragments (Darveau *et al.* 1995, Schmiegelow *et al.* 1997). Thus, squirrels could have a considerable impact on nest survival if songbird densities increase, even temporarily, as forests become fragmented. Experiments manipulating the density of nests within individual squirrel territories are required to test the functional response of red squirrels to increasing nest densities.

# CHAPTER 4. General Conclusion: A predator's perspective of nest predation.

The purpose of this study was to relate predation on songbird nests by red squirrels to the behavioural characteristics of individual squirrels at a forest edge. Previous studies have suggested that aspects of predation are explained by the habitat use, activity and search mechanisms of predators (Tinbergen *et al.* 1967, Martin 1988, 1993, Andrén 1992, Sieving and Willson 1998). However, there have been few direct tests of the mechanisms underlying the searching success of predators. In Chapter 2, I described how red squirrels selected forest edge habitat in late spring and early summer. Selection of edges was probably due to increased abundance of spruce buds at edges. In Chapter 3, I reported that, despite frequent use of edges, squirrels did not find artificial nests faster at forest edge than in interior forest locations. Further, nest survival was not related to previous use of nest sites or nesting microhabitat by red squirrels. Squirrels did, however, learn to search for second nests on their territory. I could not determine how squirrels located artificial nests. Squirrels returned to nest sites after quail eggs were taken, but did not change their activity at larger spatial scales. Therefore, neither area-restricted search nor nest microhabitat search cues appear to explain how squirrels were able to locate successive nests efficiently.

## Searching behaviour of red squirrels

If predation on songbird nests is incidental, nest survival should be related to the activity of predators. How and where red squirrels forage is associated with the seasonal abundance of foods. In spring and early summer, when cone stores are low, squirrels use a variety of food items (Brink and Dean 1966, Ferron *et al.* 1986) and tend to return to profitable habitats (e.g., edges) or locations (Ferron *et al.* 1986, Wauters *et al.* 1992, Benhamou 1996). Others have also reported that the searching to feeding ratio of squirrels is highest during this period (Ferron *et al.* 1986, Benhamou 1996). As the abundances of cones and mushrooms increase later in the season, squirrels focus their activity on harvesting and caching these items for winter use. Spatial memory and a limited area-restricted search are likely used by squirrels to relocate and forage within profitable food patches in their territory.

Although I did not find a relationship between the location of squirrel activity and nest survival, predation on nests by squirrels may initially have been incidental. How squirrels

forage likely influences the probability of detecting a nest. Red squirrels may depredate nests, regardless of location, simply because the songbird breeding season is concurrent with the time of low cone stores and increased searching by squirrels. Also, squirrels may search for nests using the same methods (area-restricted searching or spatial memory) used for more common foods. Using these search mechanisms, squirrels would revisit nest sites. Spatial memory of predators could explain why birds abandon disturbed nests, and, following nest failure, renest in new locations (e.g., Sonerud 1985). Still, not all predation by squirrels was incidental. Once a nest was found, squirrels became more efficient predators. Alternate search mechanisms, perhaps olfactory cues, are probably used by squirrels to locate successive nests on their territory.

## Forest fragmentation and nest predation

An increase in the diversity, abundance and activity of predators at forest edges is thought to explain elevated rates of nest predation at edges. Increased predator diversity likely has the greatest impact on predation at edges. Most evidence for increased predation at edges comes from studies in agricultural landscapes where predator diversity is high (Andrén 1995). Here I found that high levels of squirrel activity at edges did not reduce the survival of nests at forest edges. I further suggested that selection of a forest-pipeline edge could have little effect on the abundance, survival or reproduction of individual squirrels at edges. Moreover, if conifer seed production is altered, the fitness and density of squirrels may be reduced in landscapes fragmented by forestry or agriculture.

Most nest predation studies relate nest survival to the abundance of particular predator species in the study area (e.g., Marini *et al.* 1995, Bayne and Hobson 1997a). I suggested that, for red squirrels, predation rates are more closely related to the number of nests within a squirrel territory. Thus, if nest densities are higher at forest edges or in fragments, predation rates may increase due to density dependent predation by red squirrels. Indeed, this is the original prediction of the ecological trap hypothesis (Gates and Gysel 1978). However, for territorial species such as red squirrels, there may be no relationship, or even a negative one, between predator abundance and predation rates. The probability of a squirrel finding a nest, and learning to find successive nests on its territory, should increase as nest density increases. However, as squirrels increase in abundance in a given area, territory size and thus the number

of nests per territory should decrease. Therefore, predation rates may actually be higher where squirrel abundance is low and territory sizes are larger. This hypothesis makes several assumptions and obviously requires further testing. The proportion of area covered per unit time by squirrels may vary with territory size and among habitats. However, at the very least, correlations between the abundance of territorial species and nest survival should be interpreted with caution.

## Artificial nests and future research

Here I show that squirrels actively search for artificial nests. This is one of the first studies to demonstrate that individual predators learn to find nests. Future studies should continue to focus on the behaviour of individual predators to clearly identify factors influencing nest survival. In particular, additional work is needed to test whether squirrels and other predators learn to find natural songbird nests. Artificial nests are useful when comparing relative predation rates among habitats or treatments (Andrén 1995). However predation rates can differ between natural and artificial nests (Willebrand and Marcstrom 1988, Major and Kendal 1996, Sloan *et al.* 1998) and predators may use different mechanisms to locate natural and artificial nests. Human scent may be used by predators to locate artificial nests (Whelan *et al.* 1994, Sloan *et al.* 1998) and predators may cue into the calls, movements or scent of parents and chicks in natural nests. Nevertheless, artificial nests have allowed researchers to effectively manipulate and identify factors influencing nest survival; most of these manipulations would have been impossible using natural nests. Results from artificial nest experiments can be used to focus research on natural nesting success.

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**Appendix 1.** List of all red squirrel behaviour and location categories recorded in each "first seen" point sample and at each 30 s sampling point during focal animal sampling.

| Variable | Details of behaviour or location recorded |
|---|---|
| **Behaviour** | |
| feeding | food item |
| foraging | food item/foraging substrate |
| traveling | |
| vocalizing | type of vocalization (rattle, bark, squeak, screech, wheeze) |
| in nest | |
| caching | food item/caching location |
| resting/vigilant | |
| grooming | |
| interaction with another squirrel | identity of other squirrel if known |
| nest building/maintenance | |
| scent marking | |
| not visible | |
| foot stomping | |
| | |
| **Location** | |
| grid coordinates | based on study grid with 30 m separating grid points, each 30 m interval was separated into ten 3 m units (e.g., A.3, 4.2) |
| distance to forest edge | 8 categories: on pipeline, between pipeline and forest, 0-3m, 3-6m, 6-9m, 9-12m, 12-30m, >30m |
| substrate | ground, midden, shrub, deadfall, snag, white spruce, aspen |
| height in tree/height of tree | estimated to nearest 1m |
| direction | facing forest edge, facing away from edge, perpendicular to edge |
| sun exposure | in sun, not in sun, cloudy |

**Appendix 2:** Description of red squirrel behaviour categories used for behaviour summaries and data analysis.

| | |
|---|---|
| **Foraging** | |
| feeding | squirrel is handling or ingesting food item |
| foraging | squirrel appears to search for food items, characterized by slow movements, frequents turns, nose close to substrate |
| caching | squirrel travels with a food item or places a food item in a ground hole, in or on a grass nest, or on a tree branch (midden caching is classified as "midden") |
| Traveling | squirrel moves rapidly from one location to another with little turning, head is usually up |
| Willow activity | squirrel is traveling on, or feeding or foraging off of, a willow shrub |
| Midden activity | any squirrel activity occurring on or in the midden where the squirrel does not remain in the nest for longer than 4 minutes. |
| Vigilant | squirrel is sitting or standing with head up, often associated with bark vocalization |
| Vocalizing | squirrel is not obviously engaged in another activity at the same time vocalization occurs, if simultaneous feeding, foraging or traveling activities occur the observation is classified as that activity rather than vocalizing |
| Other | includes resting (head down on substrate, eyes closed), interactions with other squirrels/species, grooming, scent marking etc. |

**Appendix 3.** Habitat selection coefficients (95% confidence interval) for the habitat use of red squirrels within territories for 1996 and three time periods in 1997. Coefficients represent the ratio of habitat use to availability within territories, see text and Manly *et al.* (1993) for calculations. * 95% confidence intervals not containing 1 indicate significant selection (>1) or avoidance (<1).

| Habitat | May 14 - July 22 1996 | May 10-31 1997 | June 25 - July 19 1997 | August 7-18 1997 |
|---|---|---|---|---|
| Forest edge | 1.70* (1.3 - 2.09) | 2.20* (1.18-3.22) | 2.13* (1.63-2.64) | 1.73 (0.75-2.7) |
| Forest interior | 0.81 (0.52 - 1.11) | 0.91 (0.2-1.63) | 0.52* (0.24-0.8) | 0.47* (0.18-0.76) |
| General forest | 0.76* (0.56 - 0.96) | 0.54* (0.26-0.82) | 0.67* (0.44-0.89) | 0.78 (0.52-1.05) |
| Midden | 19.91* (10.05 - 29.76) | 16.97* (2.77-31.18) | 19.91* (6.09-33.74) | 25.46* (13.47-37.44) |
| Shrub/ Pipeline | 0.17* (0.01 - 0.33) | 0.00* (0-0) | 0.13* (0-0.27) | 0.08* (-0.05-0.2) |

**Appendix 4.** Comparison of observed and expected frequencies of categories of red squirrel behaviour among forest edge, forest interior and general forest habitats for May 14-July 22, 1996. Goodness of fit tests were performed only when at least 4 of the 6 observed and expected categories had counts greater than 5 (Sokal and Rohlf 1995). The null hypothesis is that each activity occurs with equal frequency across habitats. Thus, expected frequencies are the average frequency of each activity over all habitat classes.

| | Observed Frequency (%) | | | Expected (%) | $X^2$ | p |
|---|---|---|---|---|---|---|
| | Edge | Interior | General Forest | | | |
| **General categories**[a] | | | | | | |
| Foraging | | | | | | |
| Tree | 38.7 | 37.2 | 23.0 | 28.6 | 10.3[a] | 0.006 |
| Ground | 7.1 | 14.1 | 8.6 | 10.3 | 3.3 | 0.192 |
| Traveling | | | | | | |
| Ground | 9.5 | 12.8 | 14.4 | 12.6 | 1.8 | 0.166 |
| Tree | 14.9 | 7.7 | 17.2 | 14.5 | 3.6 | 0.412 |
| Vigilant | 8.3 | 10.3 | 14.4 | 10.5 | 3.8 | 0.154 |
| Vocalizing | 14.3 | 12.8 | 14.4 | 15.4 | 0.6 | 0.745 |
| Other | 7.1 | 5.1 | 8.1 | 7.2 | | |
| **Food Categories**[b, c] | | | | | | |
| Spruce buds (tree) | 23.2 | 24.4 | 10.0 | 16.3 | 13.1 | 0.001 |
| Willow (willow) | 2.4 | 1.3 | 2.4 | 2.4 | | |
| Old cones | 2.4 | 5.1 | 4.3 | 5.4 | | |
| New cones | 12.5 | 2.6 | 6.7 | 7.0 | 9.5 | 0.009 |
| Other | | | | | | |
| ground | 4.8 | 11.5 | 6.2 | 6.1 | 4.25 | 0.119 |
| tree | 3.6 | 7.7 | 3.3 | 4.0 | 2.93 | 0.231 |
| Non-food activity | 51.2 | 47.4 | 67.0 | 58.7 | 5.75 | 0.057 |
| **N** | 168 | 78 | 209 | | | |

[a] $\alpha=0.008$ (Bonferonni adjustment for 6 comparisons); [b] $\alpha=0.01$ (5 comparisons); [c] due to small numbers of observations, ground and tree old and new cone activities were pooled, and fungi feeding, foraging or caching activities were pooled with "other" ground or "other" tree categories.

**Appendix 5.** Comparison of observed and expected frequencies of red squirrel behaviour categories among forest edge, forest interior and general forest habitats for May 10 to August 18, 1997. Goodness of fit tests were performed only when at least 4 of the 6 observed and expected categories had counts greater than 5 (Sokal and Rohlf 1995). The null hypothesis is that each activity occurs with equal frequency across habitats. Thus, expected frequencies are the average frequency of each activity over all habitat classes.

| | Observed Frequency (%) | | | Expected (%) | $X^2$ | p |
|---|---|---|---|---|---|---|
| | Edge | Interior | General Forest | | | |
| **General categories**[a] | | | | | | |
| **Foraging** | | | | | | |
| Tree | 43.3 | 45.2 | 33.3 | 36.0 | 3.0a | 0.23 |
| Ground | 17.8 | 21.4 | 23.3 | 20.6 | 0.7 | 0.69 |
| Traveling | | | | | | |
| Ground | 8.3 | 14.3 | 12.4 | 11.4 | 1.7 | 0.42 |
| Tree | 8.3 | 0.0 | 11.6 | 9.0 | | |
| Vigilant | 6.4 | 2.4 | 6.2 | 7.0 | | |
| Vocalizing | 8.3 | 9.5 | 3.9 | 6.6 | | |
| Other | 7.6 | 7.1 | 9.3 | 9.4 | 0.7 | 0.71 |
| **Food Categories**[b] | | | | | | |
| Spruce buds (tree) | 14.0 | 23.8 | 3.9 | 10.7 | 6.3 | 0.04 |
| Willow (willow) | 3.2 | 0.0 | 0.8 | 1.7 | | |
| Old cones** | 1.9 | 7.1 | 3.1 | 7.1 | | |
| New cones* | | | | | | |
| Ground | 1.9 | 4.8 | 3.1 | 3.5 | | |
| Tree | 10.2 | 4.8 | 5.4 | 6.2 | 4.6 | 0.10 |
| Fungi | | | | | | |
| Ground | 3.2 | 0.0 | 1.6 | 2.8 | | |
| Tree | 2.5 | 2.4 | 4.7 | 2.8 | | |
| Other | | | | | | |
| Ground | 11.5 | 11.9 | 17.1 | 13.0 | 1.8 | 0.41 |
| Tree | 14.6 | 11.9 | 17.8 | 12.4 | 2.6 | 0.27 |
| Non-food activity | 36.9 | 33.3 | 42.6 | 39.9 | 0.8 | 0.66 |
| | | | | | | |
| N | 157 | 42 | 129 | | | |

[a] $\alpha=0.013$ (Bonferonni adjustment for 4 comparisons); [b] $\alpha=0.010$ (5 comparisons)
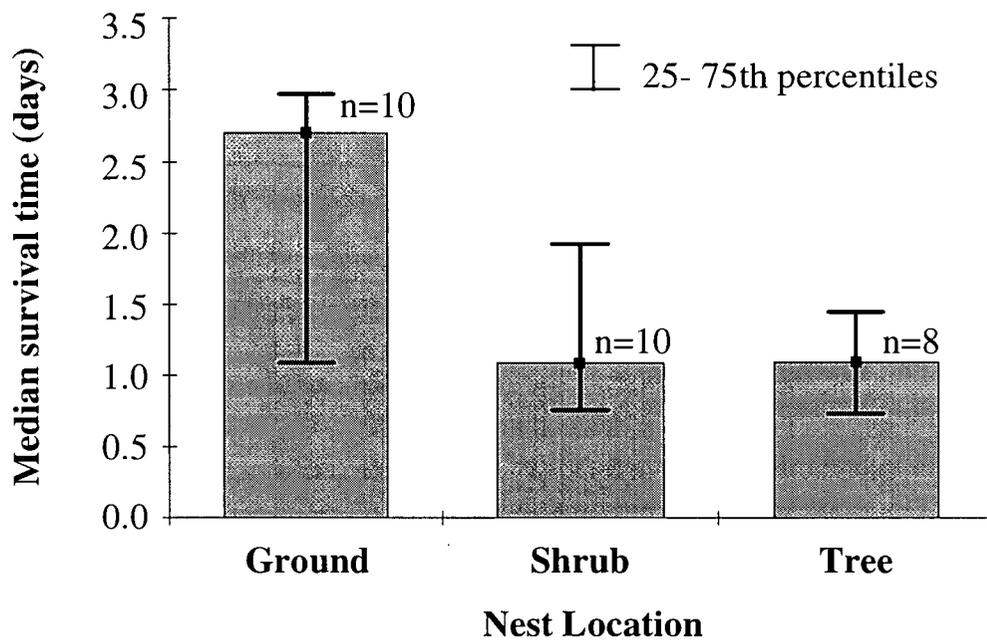
**Appendix 6.** Comparison of nest survival among ground, shrub and tree locations. Survival was defined as the time to first nest disturbance by any predator species. Results are from trials of artificial nest experiments conducted in June-July, 1996. In this trial nests were placed in one of the above locations in each of 30 red squirrel territories. One shrub and one tree nest were not disturbed during the experiment and were not included in the above summary.

**Appendix 7.** List of species that may depredate songbird nests in the Kluane Lake, YT study area.

| Small mammals (herbivores) | Carnivores |
| --- | --- |
| Red squirrel (*Tamiasciurus hudsonicus*)* | Short-tailed weasel (*Mustela erminea*)* |
| Arctic ground squirrel (*Spermophilus parryi*)* | Least weasel (*Mustela nivalis*)* |
| Northern flying squirrel (*Glaucomys sabrinus*) | Marten (*Martes americana*) |
| Least chipmunk (*Eutamias minus*)* | Mink (*Mustela vison*) |
| Deer mouse (*Peromyscus maniculatus*)* | Wolverine (*Gulo gulo*) |
| Meadow vole (*Microtus pennsylvanicus*)* | Lynx (*Lynx canadensis*) |
| Red-backed vole (*Clethrionomys rutilus*)* | Wolf (*Canis lupus* ) |
| Bushy-tailed woodrat (*Neotoma cinerea*) | Coyote (*Canis lutrans*) |
| Porcupine (*Erethizon dorsatum*) | Red fox (*Vulpes vulpes*) |
| Snowshoe hare (*Lepus americanus*)* | Black bear (*Ursus americanus*) |
| | Grizzly bear (*Ursus arctos*) |

**Birds**
Grey jay (*Perisoreus canadensis*)*
Magpie (*Pica pica*)*
Common raven (*Corvus corax*)

* plasticine dentition patterns were available from museum skulls or live animals for these species