University of Alberta

Relationships Between Northern Flying Squirrels (*Glaucomys sabrinus*), Stand Age and Stand Structure in Aspen Mixedwood Forests of Alberta

by

Lisa Diana McDonald

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degrees of Master of Science

Department of Biological Sciences

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Relationships Between Northern Flying Squirrels (*Glaucomys sabrinus*), Stand Age and Stand Structure in Aspen Mixedwood Forests of Alberta submitted by Lisa Diana McDonald in partial fulfillment of the requirements for the degree of Master of Science

Dr. Stan Boutin, Supervisor

Dr. Jan O. Murie, Committee Member

Dr. Randy Currah, Committee Member

September 27/96

Dedication

To Karl Larsen

For helping me believe I could do this.

Abstract

I studied relative abundance, vegetation associations and den selection of northern flying squirrels in three age classes of aspen mixedwood stands. In two years of study, number of squirrels captured/1000 trap nights was 5.7 and 5.4 in four old (122-146yrs), 1.1 and 0.8 in four mature (51-63yrs), and 3.4 and 0.8 in four young stands (23-26yrs). Logistic regression models showed number of large diameter snags, birch and conifers were correlated with presence of flying squirrels.

Characteristics of 78 dens were measured. Flying squirrels were commonly found in excavated cavities facing a southerly direction. Cavities were typically located in tall, large diameter aspen snags or live trees. Den tree and cavity characteristics were compared to what was available across stand ages. Squirrels selected snags with cavities over live trees with cavities, but did not select specific snag characteristics. Single cavities on a tree and large entrances were selected cavity characteristics.

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My parents, Ken and Sheila McDonald, deserve much credit for inspiring my love and respect of nature. I have many fond memories of camping trips to the mountains, north to Lac la Biche and Long Lake and to the west coast. As a youngster, I never understood why you made us clean up campsites even when it wasn't our garbage, but now I do and am thankful for it.

Most of all, I thank my husband David Verbisky, who patiently listened without judgment when I just needed to vent my frustrations. However, I am starting to suspect that you weren't all that interested in flying squirrels when we first met. I'm probably the only woman that pick-up line would work on!

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Chapter I.

Introduction

How do we conserve biodiversity in harvest regenerated forests? This question is commonly asked today (DesGranges and Rondeau 1992; Thompson 1992) as research interests are piqued by the challenge of maintaining the integrity of the boreal ecosystem while resource extraction continues and expands. Large tracts of forested land are slated for timber harvest in Alberta's aspen mixedwood forests (Alberta Lands and Forest Service 1994). Intensive harvesting of hardwoods has the potential to change biodiversity and forest structure at a landscape scale as well as at a stand scale.

Before we can understand the effects of large-scale timber harvesting, there is a need to establish a template for what occurs in naturally regenerated forests in terms of structure and biodiversity. This template may provide a control for future studies and a reference point to measure our success at maintaining biodiversity and structure in harvest regenerated forests. Ideally, such templates would consist of studies examining forest structure and biodiversity at both the landscape and stand scale.

Although broad community based studies examining structure, composition and biodiversity are valuable, it is also useful to focus on single species for study. Studying habitat use by a single species helps humans to view habitat from the perspective of that animal, which can help us minimize the anthropogenic tendency to value, and thus conserve, only what we perceive as important. By letting the animal show us what is important to it, we may realize the importance of habitat attributes which we would have previously considered unimportant or not considered at all. Monitoring wildlife species may also allow us to determine if, by conserving tangible forest structures, we have successfully maintained the integrity of the forest.

The current study was part of a collaborative effort with the Alberta Environmental Centre to examine the relationships between, forest age, forest structure and biodiversity in aspen mixedwood forests. My contribution to this project was to examine the relationship between northern flying squirrels (*Glaucomys sabrinus*) and forest age and forest structure. I focussed my study further to examine den use and den selection by northern flying squirrels. I asked several questions, all of which were related to understanding the impacts of timber harvesting on northern flying squirrels and increasing the knowledge base for this poorly studied species.

1. Are flying squirrels more abundant in coniferous or deciduous forest types? Several studies have suggested that northern flying squirrels are more abundant in conifer dominated stands than deciduous stands (eg: Soper 1970; Maser *et al.* 1981). No studies have been done to support or refute this suggestion.

2. Are flying squirrels associated with a particular age class of forest? Timber harvest targets old stands and brings these stands into a 60 to 70 year rotation. This reduces the amount of old stands in harvest regenerated forests (Thomas *et al.* 1988; Maser 1994). Species whose greatest abundance is found in old stands could be affected negatively by present harvest strategies.

3. Are flying squirrels associated with certain vegetation variables? The opportunity exists to manipulate a number of vegetation variables at the harvest site. By knowing the vegetation variables associated with a species, we can identify whether a species might be particularly sensitive to harvesting and possibly take measures to conserve appropriate vegetation attributes at the harvest site.

4. Do flying squirrels select den trees or cavities with certain characteristics? In order to conserve flying squirrel den trees and cavities, it is beneficial to understand the components that comprise a suitable den tree as determined by selection by flying

squirrels. In this study, selection is defined as greater use than expected by relative availability and in no way implies preference or requirement. The term preference is often used to describe selection data (Loeb 1993; Ransome 1995), but I believe a distinction exists between these two terms. An animal might select a particular aspect of its habitat, but the cause of selection may be due to exclusion from a resource that offers better survival or reproductive benefits, therefore negating any implications of preference. Selection indicates only that the animal is using an aspect of its habitat that confers the best advantages (Nilsson 1984; Martin and Roper 1988; Kelly 1993) given the current environment.

In chapter II, I describe the relative abundance of flying squirrels in young, mature and old stands of aspen mixedwood forest, and associations between vegetation structures and the presence of flying squirrels in this forest type. To estimate relative abundance of flying squirrels in deciduous and coniferous forest types, I compare number of flying squirrel captures per unit effort in this study to data collected for studies done in coniferous forests. Chapter III is a more detailed examination of habitat use by northern flying squirrels at the stand scale. I focus on den use and den selection across the three stand ages. I examine selection of den sites by flying squirrels on the basis of whether the tree is live or dead and on the basis of specific snag and cavity characteristics. In this chapter, I also describe the characteristics of snags in the three stand ages in order to demonstrate how snag characteristics can differ among stand ages.

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Chapter II.

Relative Abundance and Vegetation Associations of the Northern Flying Squirrel (*Glaucomys sabrinus*) in Three Stand Ages of Aspen Mixedwood Forests

Introduction

Alberta has embarked on the development of a new natural resource industry based on the large-scale harvest of trembling aspen (*Populus tremuloides*). As stated by the Environmental Assessment Review Board in 1990, extensive areas in Alberta will be affected. In northeastern Alberta alone, Alberta-Pacific Forest Industries, Inc. (ALPAC) has been allocated a forest agreement area exceeding six million hectares.

Large-scale timber harvesting has the potential to change forest structure at a landscape scale. Optimal strategies for logging companies, such as ALPAC, are aimed at harvesting old stands first (Maser 1994), before marketable fibre is further lost to staining and fungal infection. With years of intense timber harvesting at this rotation age (60-80 years), the age class of the forest will become truncated with young and mature stands dominating the landscape (Maser 1994). A reduction in the amount of old stands will bring a reduction in the structures typically associated with advanced seral stages. Some of these structures include large diameter trees and snags (Thomas *et al.* 1988; Tyrrell and Crow 1994) which provide nesting habitat for many wildlife species (Mannan *et al.* 1980; Rudolph *et al.* 1990; Loeb 1993). The presence and abundance of large trees and snags can influence the distribution and abundance of species associated with them. A species that is a specialist for old stands or whose greatest abundance is found in this age class could be affected negatively by a harvest strategy that reduces the amount of old forest.

Harvesting also has the potential to change forest structure at a stand scale. In naturally regenerated forests, vegetation structures often escape fire due to variation in topography, soil moisture and weather conditions that affect fire behavior (Smith *et al.* 1994). Remnant trees and snags may persist in newly regenerating stands and perhaps into mature stands, thus creating structural diversity. With clear-cut harvesting, the method commonly used by harvest companies, most large diameter trees and snags are removed from the harvest site.

Even if single trees and snags were left standing at the harvest site, they would be subject to blow down (Franklin and Forman 1987). The combination of those two events results in fewer large diameter trees and snags in harvest regenerated forests than in naturally regenerated forests. This is particularly true in the younger age classes where the presence of large diameter trees and snags is entirely dependent on remnant structures. A species that uses remnant trees and snags in young and mature stands could be negatively affected by present harvest practices. One such species might be the northern flying squirrel.

Little is known about habitat use by northern flying squirrels, particularly in broad leafed deciduous forests. Most studies of this species have been done in conifer dominated forests. Soper (1970) suggested that flying squirrels select conifer stands over deciduous stands and Maser *et al.* (1981) described the geographic distribution of these squirrels as coinciding with forests dominated by a variety of coniferous species. Subsequently, studies on flying squirrels have focused on conifer dominated forests (examples: Harris and Maser 1984; Mowrey and Zasada 1984; Maser *et al.* 1986; Rosenberg and Anthony 1992; Witt 1992; Hayward *et al.* 1993) despite findings by Weigl (1978) that northern flying squirrels did not show a preference for coniferous habitat over deciduous habitat in large outdoor pens. Although several studies (Connor 1960; Weigl and Osgood 1974; Anderson *et al.* 1980) have documented the presence of flying squirrels in hardwood forests, these studies included only a brief description of habitat use and only one (Anderson *et al.* 1980) attempted to quantify abundance of flying squirrels.

Several studies have examined habitat use by northern flying squirrels in relation to stand age. Based on comparisons of abundance between stand ages, it has been suggested that within conifer forests, flying squirrels are associated with old stands (Harris and Maser 1984; Brown 1985; Franklin 1988; Witt 1992). Other studies in conifer forests refute this idea by providing evidence that flying squirrels inhabit all stand ages equally (Anthony *et al.*

1987; Aubry *et al.* 1991; Corn and Bury 1991; Gilbert and Allwine 1991; Rosenberg and Anthony 1992). The question remains as to whether or not northern flying squirrels are associated with old growth stands. Determining the relative abundance of flying squirrels in three age classes of aspen dominated forests will help clarify the issue on stand age use by flying squirrels and determine if a pattern exists in this alternate habitat types.

Little is known about vegetation attributes associated with northern flying squirrels, particularly in hardwood forests. In conifer dominated forests several studies found flying squirrels to be positively associated with density of spruce, birch, tall snags>10cm DBH, shorter snags with an advanced decay class, fine litter and lower densities of moss (Payne *et al.* 1989; Corn and Bury 1991; Gilbert and Allwine 1991). No correlation was found with understory characteristics (Payne *et al.* 1989) and, in one case, none of the vegetation variables measured were correlated with flying squirrel densities (Rosenberg and Anthony 1992). The results are inconsistent among studies, with large diameter snags being the only vegetation variable associated with flying squirrels in more than one study (Corn and Bury 1991; Gilbert and Allwine 1991). Further study is needed to determine if large snags are consistently a habitat component associated with flying squirrels and to determine if this association persists across broad habitat types.

By understanding habitat use of northern flying squirrels in terms of forest type and age class and the vegetation attributes associated with them, we can begin to understand how to manage effectively for this species at the landscape and stand scale in aspen dominated forests slated for timber harvest. The purpose of this study was to determine relative abundance of flying squirrels in aspen mixedwood stands of different ages and to determine which vegetation attributes were associated with the presence of squirrels. Relative abundance data were also compared to studies done in conifer dominated forests to determine if flying squirrels were more abundant in one forest type over another.

Methods

I) Study Area

Study sites were located in aspen mixedwood boreal forests of northeastern Alberta in the Lac la Biche area (55°, 112°). Young stands were located near Wandering River and mature and old stands were located near Heart Lake and Touchwood Lake (Figure 1.1). Most stands were within Alberta Pacific Forest Company's forest management area. These study sites, and the subsequent study, were part of a large biodiversity project done by the Wildlife Ecology Branch of the Alberta Environmental Centre in Vegreville.

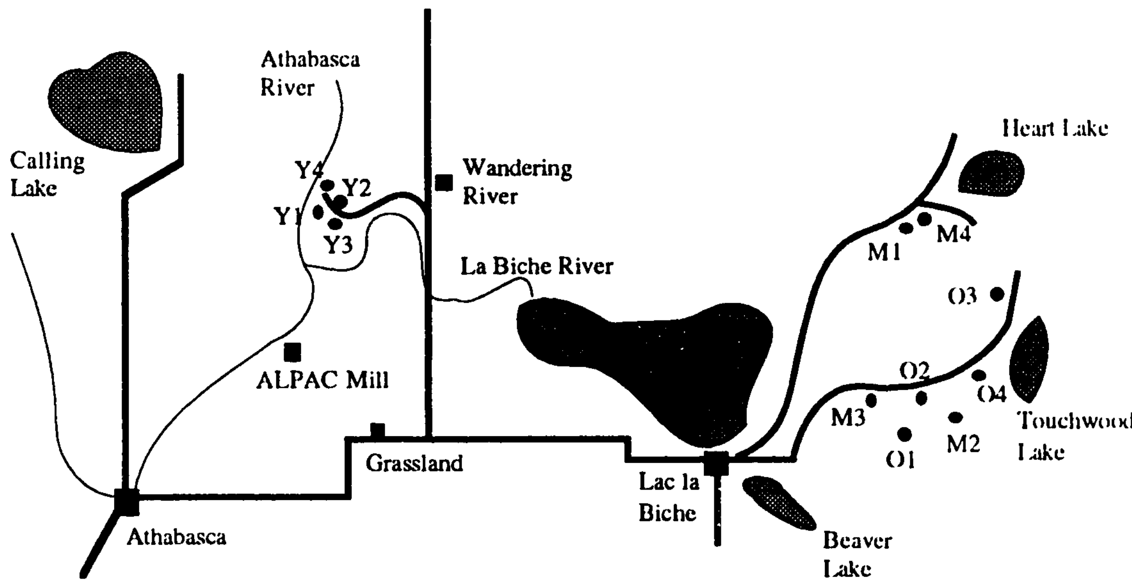

Figure 1.1 Schematic diagram of research stands in Alberta. Y=young stands, M=mature stands and O=old stands.

Twelve 100 ha aspen dominated stands were sampled: four young (23-26 yrs), four mature (51-63 yrs) and four old (122-146 yrs). Stand age was determined by fire history records, aerial photography, ground truthing and tree core samples. Within each stand, six sites were located randomly inside a 100 m buffer strip from the stand-edge. Each site (100 m radius) was permanently marked at its centre.

All stands had regenerated naturally after fire disturbance. Young stands were dominated by small diameter (approx. 10 cm) aspen saplings mixed with balsam poplar (*Populus balsamifera*) saplings. White spruce (*Picea glauca*) seedlings were also present. Many small diameter snags (<10 cm DBH) within the stand originated from self thinning. Large diameter snags were also present and appeared, from their large diameter, to be remnants from the previous stand. Small meadows consisting largely of tall grasses and willow (*Salix* spp.) were also present in young stands.

Mature stands were characterized by an overall uniformity in structure. The canopy was closed; consequently, little understory was present. Snags were mainly generated from self thinning as evident from the similar diameter to that of the live trees present. Mature stands were dominated by aspen trees mixed with balsam poplar between 10 and 20 cm in diameter. Groves of small diameter (approx. 5-10 cm DBH) white spruce existed within these stands.

Old stands were dominated by aspen trees mixed with balsam poplar. White spruce were also present and birch trees became more prominent at this stand age. The canopy was more open than in mature stands with a greater amount of structural diversity. The understory was well developed and consisted largely of rose (*Rosa acicularis*) and alder (*Alnus crispa*) as well as regenerating aspen and balsam saplings. Both newly dead and highly decayed snags were present which presumably originated after the last fire rather than before the fire.

II) Trapping Data

Flying squirrels were live-trapped for six weeks between July 1 and August 22, 1993. Traps were set for three consecutive nights each week in four young, four mature and four old stands. In 1994, two young, two mature and two old stands were re-sampled between

May 3 and May 28. In each stand, squirrels were live-trapped for three consecutive nights followed by three nights when traps were baited and fixed open. This session was followed by six consecutive nights of trapping giving a total of nine nights of trapping for each stand.

At each site, four traps were placed along each of three randomly chosen 80 m transects extending from the site centre, thus constituting 12 traps per site (Figure 1.1). Traps (Tomahawk model 201; 40 cm x14 cm x 16 cm) were positioned within a semi-circle (10 m radius) that extended forward along a transect at 20 m intervals. Within the semi-circle, trap placement was chosen based on the following hierarchy: largest diameter conifer (>20 cm DBH), followed by the largest diameter snag (>20 cm DBH), followed by largest diameter deciduous tree. At the chosen location, a trap was nailed horizontally to the tree between 1.5 and 2.0 m above ground with the mouth of the trap as close as possible to the tree trunk. To provide cover for captured animals, cardboard boxes were constructed to fit over the end of each trap. Polyester filling placed at the back of the trap was provided for bedding material. Traps were baited with a mixture of peanut butter, molasses and rolled oats and a piece of apple.

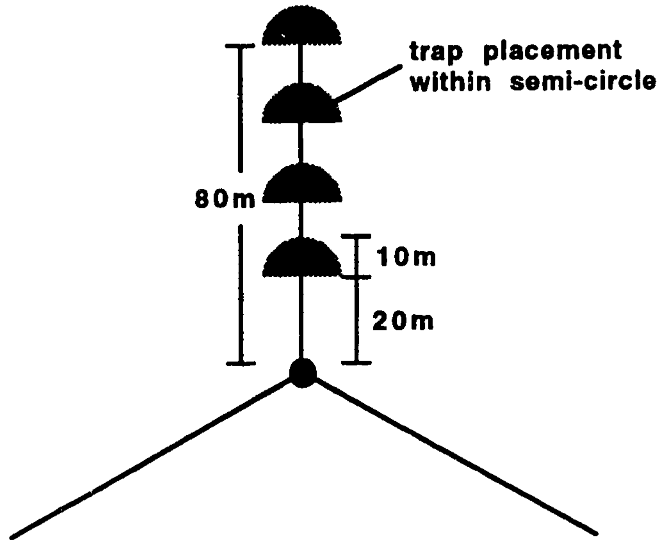

Figure 1.2. Schematic diagram of trap placement at each site. Each trap was placed within a semi-circle with a radius of 10 m. Semi-circles extended forward from points every 20 m along an 80 m transect. There were a total of 12 traps at each site with six sites in each stand for a total of 72 traps per stand.

Trapping effort in 1993 consisted of 2,592 trap nights divided equally among stands. In 1994, trapping effort totalled 3,888 trap nights divided equally among stands.

III) Vegetation Association Data

The following vegetation data were obtained from research scientists working on the Alberta Environmental Centre's Aspen Biodiversity project. Vegetation data were collected at each of the six sites located within each of 12 study stands. The following vegetation variables pertaining to this study were measured: density of snags >20 cm DBH, density of spruce >10 cm DBH, density of birch >10 cm DBH, volume of coarse down woody material >20 cm DBH, shrub density, density of aspen >20 cm DBH and density of balsam poplar >10 cm DBH. More detailed methods on vegetation data collection can be found in Lee *et al.* (1995).

Snags and Trees

Snags and trees were sampled using a nearest neighbor technique (Clark and Evans 1954). A snag was defined as a standing dead tree with a DBH>10 cm and a height >2.0 m. Only live trees that grew into the upper canopy and had a DBH greater than 10 cm were sampled. Five points no less than 20 m apart were randomly chosen at each of the six sites within each stand. From each point, the nearest snag/tree was located and its nearest neighbor. Species, height, diameter, percent bark and decay class were recorded for each tree and snag. Density was calculated from the nearest neighbor distance (Clark and Evans 1954). Ten trees and snags were sampled per site giving a total of 60 trees and 60 snags sampled per stand.

Coarse Down Woody Material

Coarse down woody material (DBH >20 cm) was sampled along four randomly placed 100 m transects extending from each of the six sites located in each stand. Stage of decay and diameter were recorded for all coarse down woody material. Length was also recorded for half of this sample. Between May and September, 1992, transects totalling 2,400 m per stand were sampled.

Tall Shrubs

Tall shrubs (1 to 3 m in height) were measured on 40 1 m x 5 m quadrats for each of the six sites located within each stand. Density of shrubs was estimated by measuring the number of stems within a quadrat.

IV) Analytical Methods

Trapping Data

Due to the skewed distribution of the data, a Kruskal-Wallis test was used to determine if there was a significant difference in number of captures of flying squirrels among stand ages. Individual stands were considered to be a sampling unit with four stands in each age class serving as replicates. Upon rejection of the null hypothesis that all age classes had an equal abundance of flying squirrels, a nonparametric Tukey-type multiple comparison test was used to determine where differences occurred (Zar 1984). Contingency analysis was used to compare trapping success between three versus six trap nights and prebaiting versus no prebaiting.

Vegetation Association Data

Capture data were also used in a stepwise logistic regression model (proc stepwise; SAS 1985) to determine which vegetation variables best explained the presence/absence of flying squirrels at the site level. For this analysis, presence was recorded for a site if one or more squirrels were captured in any of the 12 traps located at the site over the trapping period. In 1993, trap nights totalled 36 per site for a total of 864 trap nights in each of the three stand ages. In 1994, trap nights totalled 108 per site for a total of 1,296 trap nights in each stand age. Recaptured squirrels caught at different sites were included in this analysis.

For the vegetation data used in the stepwise logistic regression model, average densities were calculated at the site level for each vegetation variable for comparison to presence or absence of flying squirrels at that site. The following explanatory variables were included in a logistic regression model: volume of coarse down woody material (>20 cm DBH), density of birch (>20 cm DBH), density of trembling aspen (>20 cm DBH), median percent cover of shrubs, density of spruce, and density of snags (>20 cm DBH). I used both forward addition and backward elimination of terms. The contribution of a variable to the model was determined using the partial F test criterion (SAS 1985). A variable was retained in the model if the change in the regression sum of squares contributing to the fit of the model was significant at a probability of 0.15 and removed if not significant at this probability. Two-way interaction variables were not included in the analysis.

Results

I) Trapping Data

Relative Abundance Between Forest Types

In 1993, ten flying squirrels were captured; three in young, none in mature, and seven in old stands (Table 1.1). No recaptures were recorded. In 1994, a total of nine flying squirrels were captured with one capture in both young and mature stands and seven captures in old stands (Table 1.1). Two recaptures occurred in the old stands.

Table 1.1. Capture results and number of trap nights in 1993 and 1994. NS=not sampled.

1993					1994				
Stand Age	# Captured				Stand Age	# Captured			
Replicate	Young	Mature	Old		Replicate	Young	Mature	Old	
1	1	0	2		1	0	1	4	
2	1	0	1		2	NS	0	NS	
3	1	0	1		3	NS	NS	NS	
4	0	0	3		4	1	NS	3	
# of trap nights	864 +	864 +	864	2,592	# of trap nights	1296 +	1296 +	1296	= 3,888

Recapture rates in both trapping sessions were too low to calculate density estimates. Instead of calculating flying squirrel densities, capture success per 1000 trap nights was used to compare relative abundance of flying squirrels between aspen dominated stands and studies done in conifer dominated stands (Volz 1986; Rosenberg and Anthony 1992; Witt 1992; Table 1.2).

Table 1.2. Number of flying squirrel captures per unit effort in deciduous and coniferous stands of different ages. Conifer data was obtained from the literature.

Author and Year of Study	Forest Type	Age Class of Stand	# of Stands	# Captured per 1000 Trap Nights
present study (1994)	aspen	old	2	5.4
present study (1994)	aspen	mature	2	0.77
present study (1994)	aspen	young	2	0.77
present study (1993)	aspen	old	4	8.1
present study (1993)	aspen	mature	4	0.0
present study (1993)	aspen	young	4	3.5
Rosenberg (1989)	Douglas-fir	old	5	15.7
Rosenberg (1989)	Douglas-fir	mature	5	13.5
Rosenberg (1988)	Douglas-fir	old	5	17.1
Rosenberg (1988)	Douglas-fir	mature	5	15.9
Volz (1985)	Western Hemlock	old	2	14.7
Volz (1985)	Western Hemlock	mature	2[1]	5.7
Witt (1981-1986)	Douglas-fir	old	2	14.7
Witt (1981-1986)	Douglas-fir	mature	5[2]	5.7

[1]One of two mature stands were regenerated from clear-cut harvest sites.
[2]Four of five mature stands were regenerated from clear-cut harvest sites.

In old conifer stands, the lowest index reported for flying squirrels captured per 1000 trap nights (Volz 1986; Witt 1992) was almost two times higher than the highest capture per unit effort index in old aspen stands. Captures per unit effort were at least seventeen times higher in naturally regenerated mature conifer stands (Rosenberg and Anthony 1992) than in mature aspen stands.

Relative Abundance Among Three Stand Ages

In 1993, capture rates were 2.3 times higher in old stands than young stands and no squirrels were captured in mature stands. Number of captures differed significantly among stand ages (Kruskal-Wallis with tied ranks; $H=8.16$, $df=2$, $p<0.005$; Figure 1.3a). A significant difference was found between mature and old stands (nonparametric Tukey-type comparison; $Q_{0.05,3}$=2.84), but not between young and mature stands ($Q_{0.05,3}$=1.58) nor young and old stands ($Q_{0.05,3}$=1.27).

In 1994, capture rates were 7.0 times higher in old stands than in either mature or young stands. There was no significant difference in number of captures among stand ages (H=3.65, df=2, p>0.10; Figure 1.3b).

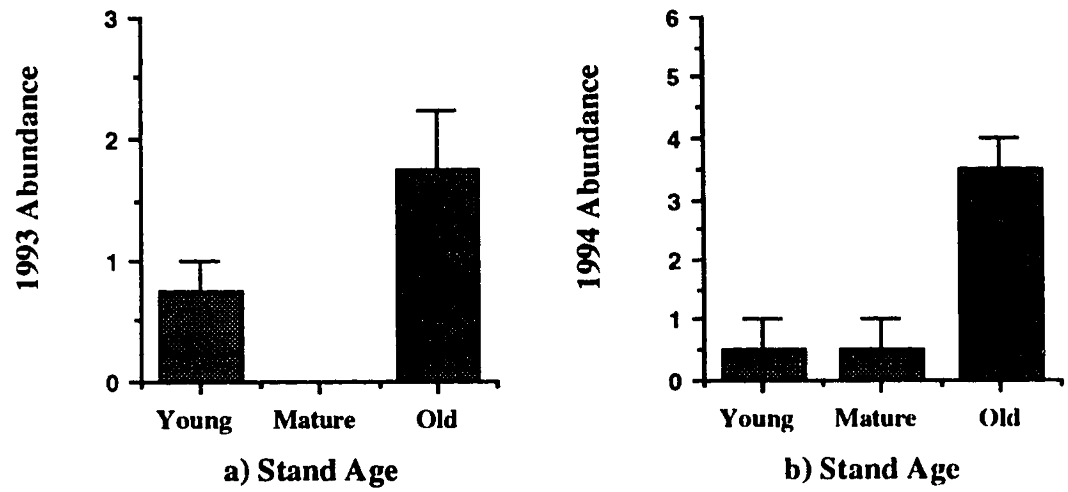

Figure 1.3. Average number of flying squirrels captured in three stand ages of aspen mixedwood forest in a) 1993 and b) 1994. Because two of four stands in each age class were logged in the winter of 1993/1994, only two stands were trapped in the summer of 1994.

Trapping Success

In 1994, the number of flying squirrel captures in three nights of trapping, with a total of 1,296 trap nights, increased from one to six with the addition of six days of pre-baiting. When the number of consecutive trap nights were doubled from three to six, there was an increase in the number of flying squirrel captures from six to eight.

Trapping success was significantly improved by prebaiting (goodness of fit test; χ^2=3.97, df=1, p=0.046) as shown by comparing capture success before and after six days of prebaiting (Table 1.3). Trapping success was not significantly improved by increasing the number of consecutive trap nights (χ^2=0.54, df=1, p=0.46) as shown by comparing capture success over three nights to six nights of trapping effort in which both were subjected to effectively six nights of prebaiting (Table 1.3).

Table 1.3. Number of flying squirrel captures for traps that were not pre-baited versus pre-baited traps and three versus six consecutive trap nights.

	No Pre-bait	Pre-bait	3 Nights	6 Nights
Capture	1	6	6	8
No Capture	1,295	1,290	1,290	2,564

III) Vegetation Association

In 1993, density of white spruce (stepwise logistic regression; F=8.5, df=70, p=0.005) and density of birch (F=3.1, df=69, p=0.085) were positively related to presence of flying squirrels (Figure 1.4a and 1.4b). Although the relationships between the response and explanatory variables were significant, the model including spruce and birch does not explain a great deal of the variation observed in the response variable (r^2=0.15).

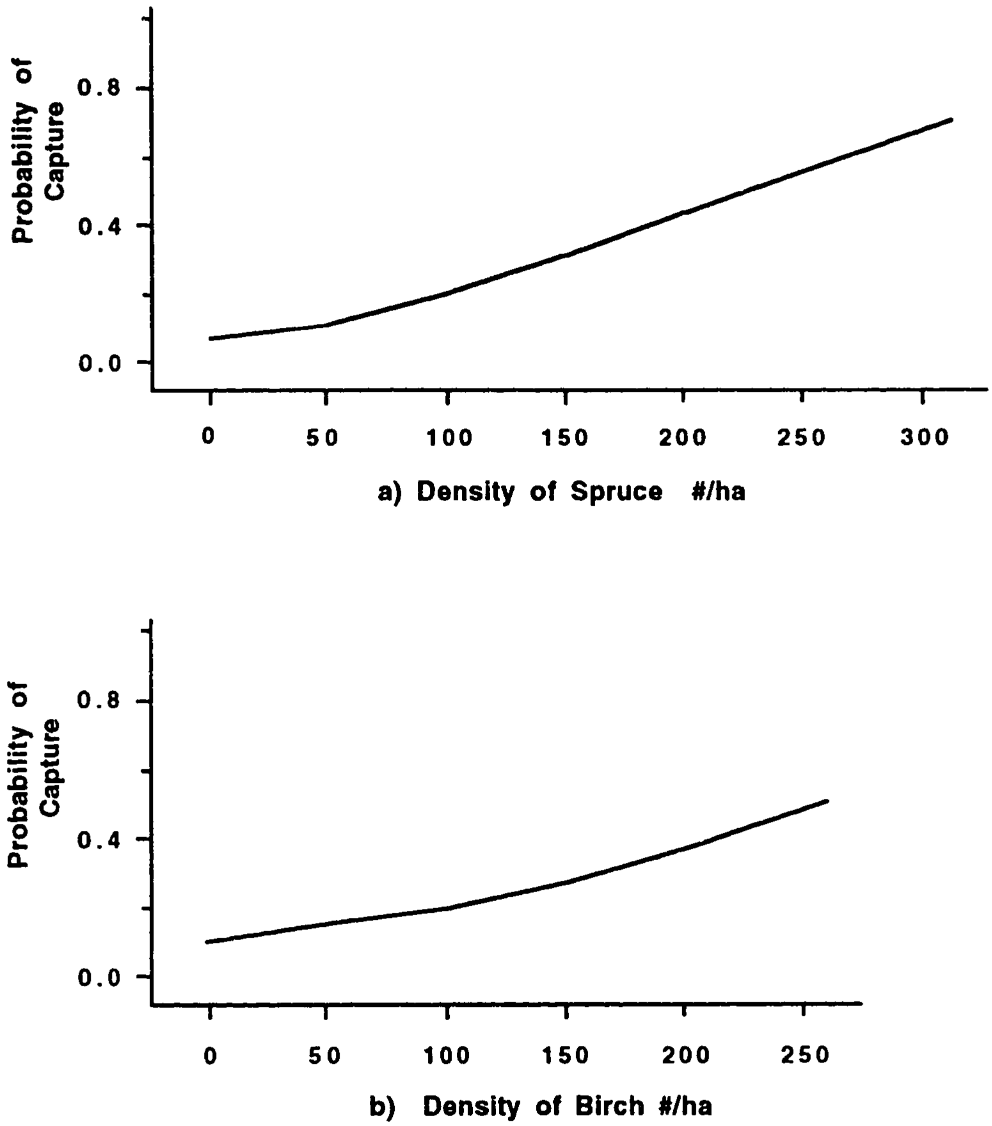

Figure 1.4. The probability of a flying squirrel capture in relation to the significant explanatory variables a) density of white spruce and b) density of birch.

Analysis was repeated for the 1993 data using only those stands that were resampled for flying squirrel abundance in 1994. Density of snags >20 cm DBH (F=5.30, df=34, p=0.028) was the only variable positively related to the presence of flying squirrels (Figure 1.5). Again, the relationship between the response and explanatory variable was significant, but the model including snags accounted for little of the variation observed in the response variable (r^2=0.14).

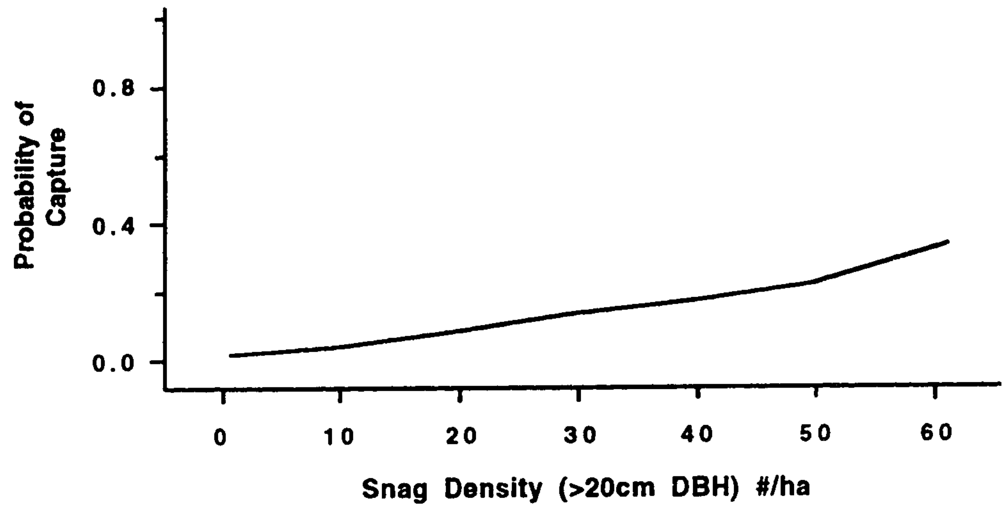

Figure 1.5. The probability of a flying squirrel capture in relation to the significant explanatory variable, density of snags >20 cm DBH.

In 1994, density of birch (F=7.80, df=34, p=0.002) and density of snags >20 cm DBH (F=2.26, df=33, p=0.052) were positively related to flying squirrel abundance (Figure 1.6a and 1.6b). The model including birch and snags accounts for a small part of the variation observed in the response variable (r^2=0.33).

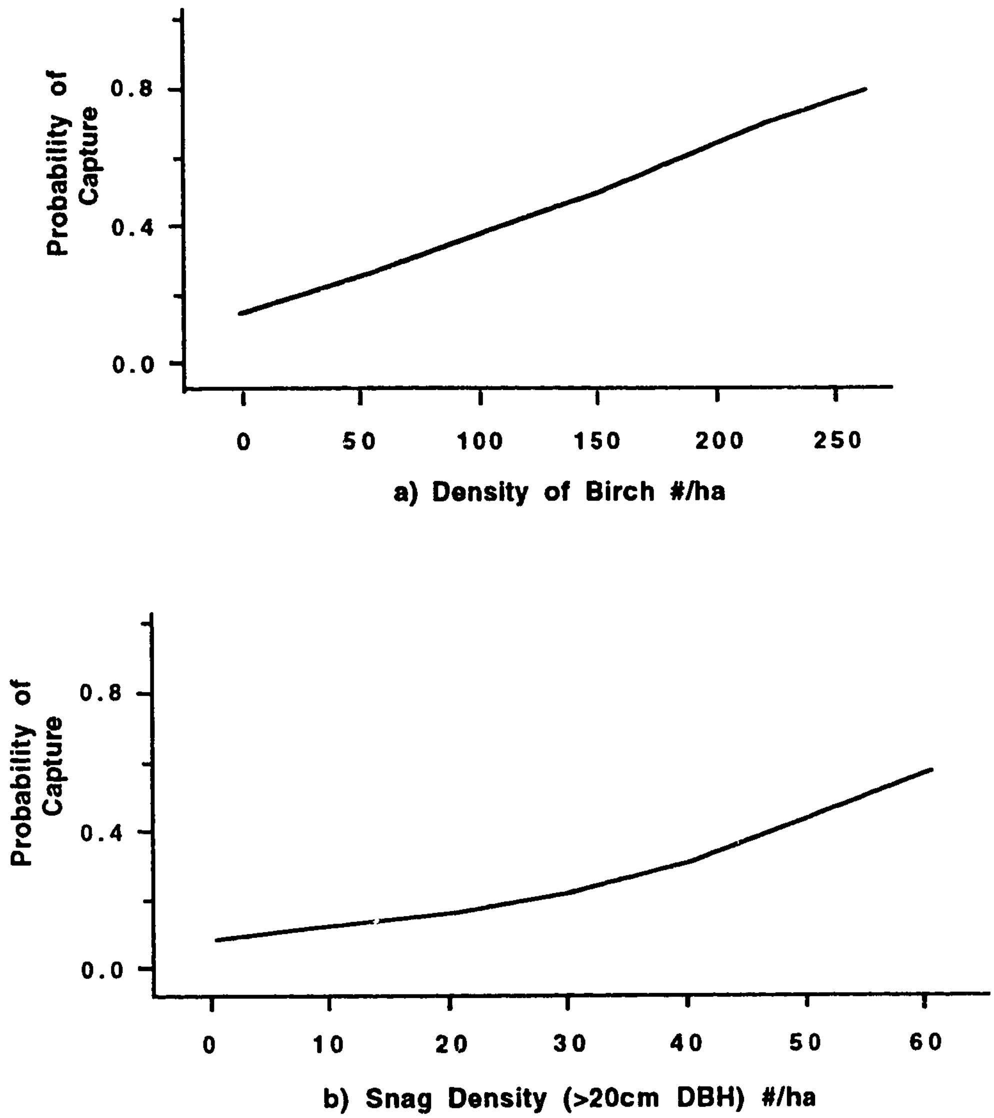

Figure 1.6. The probability of a flying squirrel capture in relation to the significant explanatory variables a) density of birch and b) density of snags >20 cm DBH.

Discussion

I) Relative Abundance Between Forest Types

In large outdoor pens, Weigl (1978) found that the more aggressive southern flying squirrel selects hardwood stands and is capable of excluding northern flying squirrels from this habitat type. This competition could account for low abundance of northern flying squirrels where these two species coexist. My study sites were located in a region of the northern flying squirrel's range where southern flying squirrels do not occur. If hardwood forests are capable of supporting a high abundance of northern flying squirrels relative to conifer stands, one would expect to see the highest abundance of this species in hardwood stands free of southern flying squirrels.

In comparison to captures per unit effort found in conifer dominated stands of the same age class (Volz 1986; Rosenberg and Anthony 1992; Witt 1992), my results indicate that northern flying squirrels in aspen stands are relatively low in abundance. Although differences in methods, location and year of study may provide some explanation for differences observed between relative numbers of flying squirrels captured in conifer versus deciduous dominated stands, these results lend support to suggestions that hardwood forests support a lower abundance of northern flying squirrels relative to conifer forests (Brown 1985).

II) Relative Abundance Among Three Stand Ages

Abundance of flying squirrels was significantly greater in old stands than in mature stands in 1993. Although a similar pattern of abundance was found in 1994, the difference between the abundance of flying squirrels in old stands versus young and mature stands was not significant. The loss of two stand age replicates in the second year of study likely reduced the power of the test to detect differences in abundance among age classes given the low number of captures. It is clear that a study of this type would require a greater number of stand age replicates to determine relative abundance among age classes of this or any rare species.

Despite the lack of significance in the second year of study, there is some evidence from these results to support suggestions that flying squirrels are associated with old growth forests (Harris and Maser 1984; Brown 1985; Franklin 1988; Witt 1992). Flying squirrel abundance was two to seven times greater in old stands than in young or mature stand. The relationship between flying squirrel abundance and stand age is likely linked to factors characteristic of forest age in general rather than to specific attributes occurring in one forest type. Structural attributes such as tall, large diameter snags, open canopy and large diameter trees that are characteristic of advanced seral stages (Tyrrell and Crow 1994) in most forest communities could be responsible for the pattern of abundance observed in this and many other studies (Harris and Maser 1984; Brown 1985; Franklin 1988; Witt 1992). This is supported by Rosenberg and Anthony (1992) who found similar densities of flying squirrels in mature and old stands, but their mature stands contained residual old growth components such as coarse down woody material, large trees and snags. Even a mature stand containing remnant attributes typical of a more advanced seral stage is capable of supporting densities of flying squirrels equal to that of an old stand.

III) Vegetation Associations

Of the variables examined, all of which that could be manipulated during harvest, density of spruce and density of birch were most strongly correlated with the presence of flying squirrels in 1993. However, when analysis was applied to only six of the 12 stands trapped in 1993, in order to facilitate comparison between the six stands trapped in 1994, the results were different. In 1993, density of snags >20cm DBH were most strongly correlated to flying squirrel abundance. These same stands in 1994 showed that flying squirrels were most strongly correlated with density of birch followed by density of snags >20cm DBH. Not only were there differences in results between years, but also between the analysis for six of 12 stands within one year.

Rosenberg and Anthony (1992) suggested flying squirrels were habitat generalists because of the lack of correlation between squirrel density and vegetation variables. I suggest the lack of consistency in my results indicates something different. Perhaps the link between trapping success and flying squirrel captures is not founded in the squirrels' relationship to foraging. Vegetation data were collected at each site and related to trapping success at that site. Squirrels were likely foraging when they were captured, therefore relationships with vegetation attributes that enhance foraging or protection while foraging would be most apparent in this correlational study. If this were the case, one might expect a strong and consistent correlation with shrubs and spruce trees. Shrubs would likely protect squirrels from predation when foraging on the ground and spruce trees are associated with the fruiting bodies of some hypogeous fungal species eaten by flying squirrels (e.g.: *Rhizopogon* spp; Trappe and Maser 1977; Maser *et al.* 1986).

If some other resource was an important determinant for the presence of flying squirrels, such as den tree availability, then a consistent relationship between vegetation variables and trapping success at a site level would not necessarily be detected. Rather than assume these results indicate that flying squirrels are habitat generalists, they might point future studies in a direction other than foraging constraints to determine what vegetation attributes are important to flying squirrels. Large diameter snags and birch trees were each correlated with squirrel captures in two of three comparisons. Correlations between flying squirrels and these vegetation variables were also found in other studies (Payne *et al.* 1989; Corn and Bury 1991). Because flying squirrels are known to den in large diameter snags and witches' brooms (Mowrey and Zasada 1984), future research might begin with examining den tree availability as a limiting factor.

In general, the models did not explain a great deal of the variation observed in the relationship between presence of flying squirrels and vegetation variables. This could indicate that the study design was not sufficiently powerful to detect vegetation associations or the relationship between flying squirrels and their habitat is dependent on different variables than were measured or variables at a different scale.

IV) Management Recommendations

Given that flying squirrels were relatively more abundant in conifer versus aspen dominated stands and the density of squirrels appears to be low in aspen dominated stands, harvest companies operating in an aspen dominated forest could use one of two approaches when managing for flying squirrels. They can manage using single species conservation or conservation of biodiversity.

The first approach might lead to not managing for flying squirrels with the assumption that populations will persist in conifer dominated stands. The second approach would likely lead to maintenance of this species at both the landscape and stand scale. Since flying squirrels are important dispersers of the spores of hypogeous fungi (Maser *et al.* 1984), it would be most prudent to employ the latter approach. These fungi form obligatory symbiotic relationships with the roots of trees and therefore are an important component in the regeneration of healthy forests (Sanders *et al.* 1975).

Ultimately, leaving continuous old forests out of rotation would likely provide the habitat needed to support flying squirrel populations. Since this is not economically feasible for forest companies, the best alternative would be to leave some old stands out of rotation and retain large diameter snags and trees at the harvest site. This practice would enhance the likelihood that flying squirrels will exist in all age classes of harvest regenerated stands of the future.

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Chapter III.

Den Use and Selection by Northern Flying Squirrels (*Glaucomys sabrinus*)
in Aspen Mixedwood Forests of Alberta

Introduction

Industrial logging has the potential to reduce the abundance of snags and trees with cavities in harvest regenerated forests. Traditionally, harvest companies target old stands and bring these stands into a rotation age that precludes the development of this older seral stage. Large diameter trees and snags are most abundant in old forests (Mannan *et al.* 1980). Because large diameter trees and snags are more likely to have cavities than small diameter trees and snags (Rosenberg *et al.* 1988), a reduction in the number of old stands will likely lead to a decrease in the number of tree cavities on the landscape. Furthermore, clearcut harvesting removes most large diameter trees and snags at the harvest site, eliminating the opportunity for these structures to persist in newly regenerating stands. In young stands created by fire, remnant trees and snags may be the only structures capable of supporting cavities. The combination of these two practices, reducing the number of old stands and clearcut harvesting, will result in a reduction in the number of snags and trees with cavities in harvested forests than in naturally regenerated forests.

Large tracts of aspen dominated forest have been slated for harvest in northeastern Alberta (Alberta Land and Forest Service 1994). Concern exists for species that use cavities in these forests because of the potential for harvesting to reduce the number of cavities in harvest regenerated forests. Nest box and natural cavity studies have demonstrated that cavity availability influences the abundance and distribution of secondary cavity users (von Haartman 1957; Mannan *et al.* 1980; Sedgwick and Knopf

1992). This may be particularly true in managed forests where abundance of food resources can remain high and abundance of nest sites is low (Nixon 1979).

Before we can understand how the availability of den sites might influence the abundance or distribution of a cavity using species, it is necessary to establish if and what den characteristics are selected by the species. It is not enough to assume that a cavity using species can use any cavity in any tree with the same degree of success. Ideally, den requirements and preferences would be used to define optimum den trees for a species. Requirements are attributes that are absolutely necessary to the survival of the animal and preferences imply that, in an ideal world void of competition, the animal would always choose that attribute in order to obtain survival and/or reproductive benefits. However, acquiring these data often necessitates time consuming experimental manipulations. Alternatively den selection can be used. Unlike requirement or preference data, selection for a characteristic indicates only that the animal is using dens with characteristic greater than expected from what is available. Studies have shown a link between animals using nest sites with selected characteristics and significantly lower nest predation rates and nest loss due to inclement weather relative to those animals in den sites without selected characteristics (Nilsson 1984; Martin and Roper 1988; Kelly 1993). Knowledge of selected den characteristics, as opposed to simply den use, allows the researcher to identify those den characteristics that impart a better chance of survival to the animal, or its offspring.

The northern flying squirrel is one species that could be affected negatively by the harvest of aspen mixedwood forests. Availability of cavities may be the primary factor limiting the abundance of this species (Volz 1986). In conifer forests, northern flying squirrels have been found to den in cavities of large diameter snags (Weigl and Osgood 1974; Maser 1981). Several studies (Harris and Maser 1984; Brown 1985; Franklin 1988; Witt 1992) have found a greater abundance of flying squirrels in old conifer stands where cavities are likely more abundant than in young or mature stands. One study (Harestad 1990) refutes this idea based on data showing higher densities of cavities than of flying squirrels, but this study was done with little knowledge of den use and no knowledge of den characteristics selected by flying squirrels.

To date, studies examining den use by northern flying squirrels have focused on coniferous forests (eg: Maser 1981; Mowrey and Zasada 1984). Although the presence of northern flying squirrels has been documented in hardwood stands (Weigl and Osgood 1974; Anderson *et al.* 1980), only incidental information on den use by flying squirrels has been reported. Apart from these studies, den use by northern flying squirrels in hardwood forests has received little attention and no study has examined den selection in either coniferous or deciduous forests.

To manage effectively for secondary cavity using species in harvest regenerated forests, it is necessary to understand the characteristics that influence cavity use by a species and the distribution and characteristics of cavities on the forested landscape. The objectives of this study were 1) to examine den tree and cavity use by northern flying squirrels in aspen mixedwood forests, 2) to determine the characteristics and distribution of trees, snags and cavities in three age classes of aspen mixedwood forest and 3) to determine den tree and cavity selection in aspen mixedwood forests.

Methods

I) Study Area

Study sites were located in aspen mixedwood boreal forests of northeastern Alberta in the Lac la Biche area (55°, 112°). Young stands were located near Wandering River and mature and old stands were located near Heart Lake and Touchwood Lake (Figure 2.1). Most stands were within Alberta Pacific Forest Company's forest management area. These study sites, and the subsequent study, were part of a large biodiversity project undertaken by the Wildlife Ecology Branch of the Alberta Environmental Centre in Vegreville.

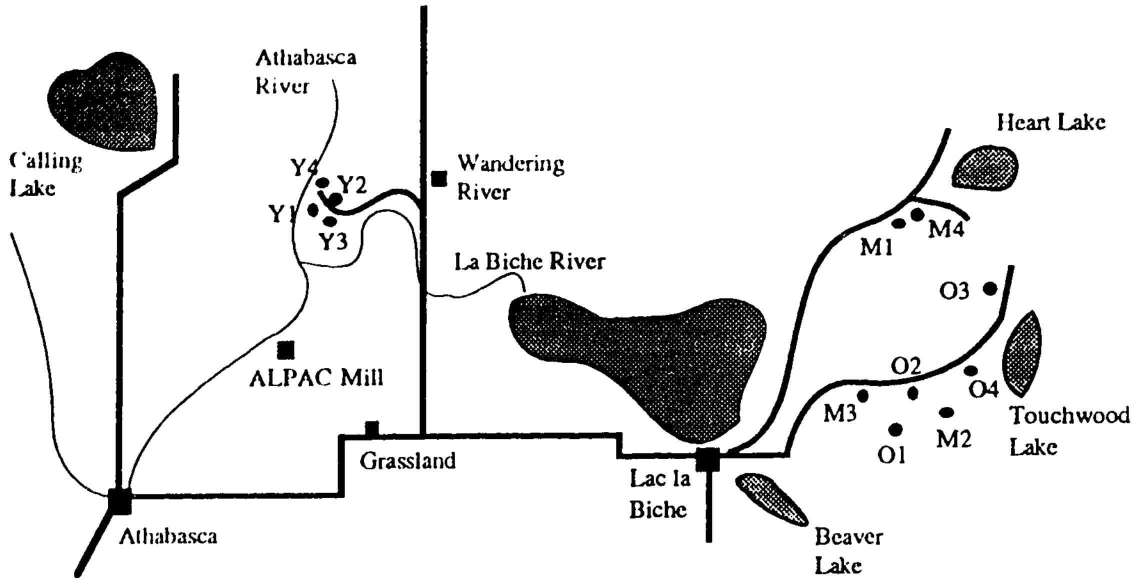

Figure 2.1 Schematic diagram of research stands in Alberta. Y=young stands, M=mature stands and O=old stands.

Twelve 100 ha aspen stands were sampled: four young (23-26 yrs), four mature (51-63 yrs) and four old (122-146 yrs) stands. Stand age was determined using fire history records, aerial photography, ground truthing and tree core samples. Within each stand, six sites were located randomly inside a 100 m buffer strip from the stand-edge. Each site (100 m radius) was permanently marked at its centre. Two stands in each age class were experimentally logged in the winter of 1993/94.

All stands had regenerated naturally after fires. Young stands were dominated by small diameter (approx. 10 cm DBH) aspen poplar (*Populus tremuloides*) saplings mixed with balsam poplar (*Populus balsamifera*) saplings of similar size. White spruce (*Picea glauca*) seedlings were also present. Many small diameter snags (≤10 cm DBH) within the stand originated from self thinning. Large diameter snags were also present and appeared from their large diameter to be remnants from the previous stand. Small meadows consisting largely of tall grasses and willow (*Salix* spp.) were also present in young stands.

Mature stands were characterized by a uniformity in structure. The canopy was closed; consequently little understory was present. Snags were mainly generated from self-thinning as evident from the similar diameter to that of the live trees present. Mature stands were dominated by aspen trees, mixed with balsam poplar, between 10 and 20 cm in diameter. Groves of small diameter (5-10 cm DBH) white spruce were present within all of these stands.

Old stands were dominated by aspen trees mixed with balsam poplar trees. White spruce were also present and birch (*Betula papyrifera*) trees were more prominent at this stand age. The canopy was more open than in mature stands with a greater amount of structural diversity present. The understory was well developed and consisted largely of rose (*Rosa acicularis*) and alder (*Alnus crispa*) as well as regenerating aspen and balsam poplar saplings. Both newly dead and highly decayed snags were present and presumably originated from within the stand as opposed to being remnant structures.

II) Characterization of Den Sites

Captured squirrels were fitted with a radio-transmitting collar (Holohil PD-2C transmitters). Squirrels radio-collared during summer of 1993 were located weekly at their daytime den sites from August to October, 1993 and biweekly from Novemeber 1993 to February, 1994. Squirrels captured in 1994 were located at their daytime den sites between May and August, 1994. At each den site, the following attributes were measured: presence of a cavity or stick nest, tree species, condition of tree (dead or alive), tree diameter (DBH), and tree height. For dens located in snags as opposed to live trees, the following characteristics were recorded; percent bark categorized as 0-20 %, 21-40 %, 41-60 %, 61-80 % or 81-100 %, bark condition described as loose or tight on the wood, and decay class based on structural attributes of the snag (Figure 2.2) such that snags with intact trunks, no leaves remaining and most of the original branches were classified as stage one. Those with intact trunks and increasingly fewer branches were classified as stage two and three. Snags with an intact trunk and no branches were classified as stage four. Relatively tall and short snags with no remaining branches and broken trunks were classified as stage five and six, respectively.

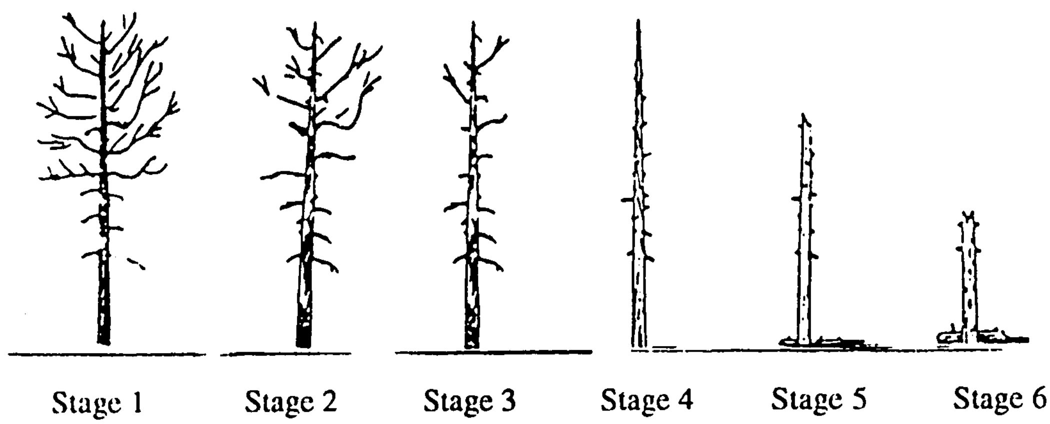

Figure 2.2. Stylized appearance of snags in six different decay stages.

Attributes of the cavity or stick nest on the den tree were recorded including, the number of entrances on the tree or snag and cavity entrance height. The type of cavity was recorded as excavated (by primary excavator), natural opening including knot holes, cracks and broken trunk tops, or constructed stick nest. Cavity entrance size was categorized as yellow-bellied sapsucker size (approx. 6 x 4 cm) or pileated woodpecker size (approx. 11 x 6 cm). Cavity entrance direction was recorded as the compass direction the entrance faced.

III) Characteristics of Trees and Snags

To determine if characteristics of den sites used by flying squirrels were different from what was available, I sampled trees and snags along eight transects in two stands within each age class. Transects were placed >100 m apart. Each transect had 10 points, 40 m apart, at which two snags and one live tree were sampled. As determined from trial sampling, a distance of 40 m between points was sufficient to avoid resampling of the same tree or snag. The closest live tree to the transect point (DBH ≥10 cm, height ≥4.0 m) was selected for sampling. If the tree had a cavity or stick nest, measurements were taken as done for flying squirrel den sites and their cavities (see above). Only diameter and tree species were recorded if no cavity or stick nest was present. If a live tree ≥10 cm DBH was not found within a 40 m radius of the sampling station, no tree was sampled. On nine of 160 occasions in young stands, no live tree ≥10 cm DBH was found within the sampling radius.

For snag sampling, the T-square nearest neighbor technique was used (Krebs 1989). The closest snag to the transect point (dead tree ≥10 cm DBH, height ≥2.0 m) was chosen for sampling. The distance between the transect point and snag was measured. The next snag measured was that which was nearest to the first snag and outside a 90° angle from the line extending from the transect point to the first snag sampled. The characteristics of all snags were measured (see above), regardless of whether or not a cavity was present. If a snag ≥10 cm DBH was not found within a 40 m radius of the sampling station, no snag was sampled. On two of 960 occasions (once in a young and once in an old stand), no snag ≥10 cm DBH was found within the sampling radius. If a cavity or stick nest was present in the live tree or snag, the characteristics of the cavity were measured (see above).

IV) Relative Abundance of Flying Squirrels

Flying squirrels were live-trapped for six weeks between July 1 and August 22, 1993. Traps were set for three consecutive nights in each of four young, four mature and four old stands. Because two of each stand age replicate were experimentally logged in the winter of 1993/1994, only the six unlogged stands were re-sampled between May 3 and May 28, 1994. In each stand, live-traps were set for three consecutive nights followed by three nights when traps were baited and fixed open. This session was followed by six consecutive nights of trapping for a total of nine nights of trapping in each stand.

At each site, four traps were placed along each of three 80 m transects extending from site centre, thus constituting 12 traps per site (Figure 2.3). Traps (Tomahawk model 201; 40 cm x 14 cm x 16 cm) were positioned within a semi-circle (10 m radius) that extended forward along the transect at 20 m intervals. Within the semi-circle, trap placement was chosen based on the following hierarchy: largest diameter conifer (>20 cm DBH), followed by largest diameter snag (>20 cm DBH), followed by largest diameter deciduous tree. For equivalent sites within the hierarchy, precedence was given to sites with trees leaning against them and/or estimated greater amounts of foliage cover by surrounding shrubs. At the chosen location, a trap was nailed horizontally to the tree 1.5 to 2.0 m above ground with the mouth of the trap as close as possible to the tree trunk. Traps were baited with a mixture of peanut butter, rolled oats, molasses and a piece of apple.

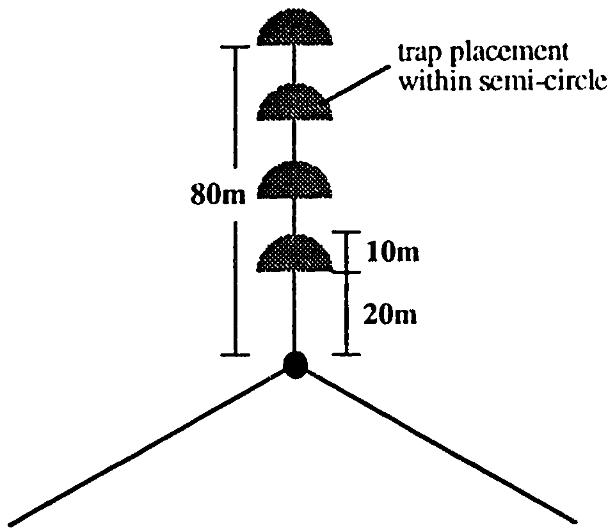

Figure 2.3. Schematic diagram of trap placement at each site. Each trap was placed within a semi-circle with a radius of 10 m. Semi-circles extended forward from points every 20 m along three 80 m transects. There were a total of 12 traps at each site with six sites in each stand for a total of 72 traps per stand.

V) Analytical Methods

Canonical discriminant function analysis (DFA; proc candisc, SAS 1985; see Pimentel 1979) was used to describe how characteristics differed between groups (see below). The Wilks' Lambda test was used to determine if the centroids for each group were significantly different at a 5% probability level. Structural coefficients were used to determine how variables contributed to the separation observed among group centroids. Whether the variable was positively or negatively associated with the canonical function significantly different at a 5% probability level. Structural coefficients were used to determine how variables contributed to the separation observed among group centroids. Whether the variable was positively or negatively associated with the canonical function was determined by the sign associated with the structural coefficient for that variable. This procedure was applied to all subsequent canonical DFA analyses.

Canonical DFA was used to determine how the following groups differed based on the variables measured: snag characteristics in three stand ages based on condition of bark, percent remaining bark, snag height, stage of structural decay, snag diameter and cavity presence; snags with and without cavities based on condition of bark, percent remaining bark, snag height, stage of structural decay and snag diameter; snags used and snags with cavities not used as den sites by flying squirrels based on condition of bark, percent remaining bark, snag height, stage of structural decay and snag diameter; and cavities used and not used by flying squirrels based on cavity type, number of cavities present on a single tree or snag, height of cavity entrance, direction the cavity entrance faced and cavity entrance size.

Due to the skewed distribution of the relative abundance data, a Kruskal-Wallis test was used to determine if there were significant differences in abundance of flying squirrels among stand ages in 1993 and 1994. Individual stands were treated as the sampling unit with two stands in each age class serving as replicates. Upon rejection of the null hypothesis that all age classes had an equal abundance, a nonparametric tukey-type comparison test (Zar 1984) was used to determine where differences occurred.

Results

Patterns of Use and Characteristics of Dens

Patterns of Den Use

I measured the characteristics of 78 den sites used by 19 flying squirrels captured in 1993 and 1994. On average, each flying squirrel used 4.1 den sites with a range of 2 to 9. Squirrels did not show a seasonal shift in sites used for dens. Of the 35 den sites located between August 1993 and February 1994, seven new dens for five of the nine flying squirrels were located after September 30. One squirrel appeared to move to a new den as a result of the original den site having been blown down in a storm rather than a spontaneous movement to a winter den. Three other squirrels moved to a new den no earlier than November 19 and one of these squirrels moved back to its September den site after this date. No subsequent locations of the other two were available as one was taken by predation and the radio collar on the other stopped transmitting. Of the remaining 28 den sites, 13 were used up to and including September 30, 1993, eight were used both before and after this date and seven were used only after September 30, 1993.

Characteristics of Den Trees and Snags

With equal trapping and den location effort among stand ages, twelve den sites were located in young stands, five in mature stands and 61 in old stands. Den cavities were found in live trees (41 %) nearly as often as snags (59 %). Because snags and live trees have inherently different characteristics, including their densities, these two groups were separated for analysis.

Most dens found in snags (81 %) originated from aspen trees. The average diamater of den snags was 36.4 ± 8.6 cm (X ± SD; range=16.3 cm to 55.5 cm). Snag height ranged from 0.7 m to 23.0 m with an average of 13.3 ± 7.1 m. Dens were typically found in highly decayed snags (65 % in decay stage 5), but most snags still had a high percentage of bark remaining on the snag (73 % had 80 to 100 % bark) and the bark was tight (50 %) as often as loose on the snag core.

Most dens found in live trees were either in aspen (58 %) or conifer (21 %) trees. Tree diameter was very similar to that of snags with an average diameter of 36.5 ± 9.9 cm (range=10.0 cm to 53.2 cm). Average tree height (21.6 ± 5.9 cm; range=10.8 m to 28.8 m) was greater in live trees than snags. This is to be expected since most of the den snags were described as structural decay category 5 which is characterized by having a broken off trunk.

Characteristics of Den Cavities

Flying squirrels used excavated cavities (48 %) almost twice as often as knothole cavities (27 %). The smaller sapsucker-sized cavities (71 %) were used more than twice as often as pileated-sized cavities. Flying squirrels tended to use a cavity when that cavity was the only one located on the den tree or snag (59 %) rather than when one (16 %), two (24 %) or three (1 %) other cavities were also present. Cavity height averaged 8.8 ± 4.6 m with a range of 0.1 m to 18.5 m. Flying squirrels used cavities that faced in a southerly direction (52 %; 135° to 224°) twice as often as cavities facing an easterly direction (20 %; 45° to 134°).

Abundance and Characteristics of Trees and Snags in Three Stand Ages

Density of Snags and Trees in Three Seral Stages

A total of 1076 snags were sampled in the three stand ages. In mature stands, the density of snags ≥10.0 cm DBH (209.8 ± 16.7 SE per ha) was six times greater than the density of snags in young stands (37.1 ± 20.0) and twice the density of snags in old stands (103.2 ± 11.2). Although snag densities were highest in mature stands, the percentage of snags with a cavity was lowest in this stand age (0.6 ± 0.0). The percentage of snags with a cavity was highest in old stands (13.0 ± 3.0) and intermediate in young stands (6.9± 3.2). As a result, the density of snags with a cavity was five times greater in old stands than young stands and ten times greater in old stands than mature stands (Table 2.1).

Table 2.1. The average density of snags and live trees (≥10.0 cm DBH) with cavities in each age class.

Stand Age	Cavity Density for Snags (ha)	Cavity Density for Live Trees (ha)	Total Cavity Density (ha)
Young	2.6	0.6	3.2
Mature	1.3	8.1	9.4
Old	13.4	15.5	28.9

The percentage of live trees with a cavity was lower in young (0.6 ± 0.7), mature (0.6 ± 0.7) and old stands (3.8 ± 0.0) as compared to the percentage of snags with a cavity in these stand ages. Given that the density of trees was higher than snags in young (105.7 ± 32.3), mature (1347.9 ± 314.2) and old stands (406.7 ± 80.1), the contribution of live trees to the overall density of cavities was considerable in mature and old stands (Table

2.1). The density of live trees with a cavity was 26 times higher in old stands than young stands and twice as high in old stands than mature stands. The overall density of cavities was three times greater in old stands than mature stands and almost three times greater in mature stands than young stands.

Differences in Snag Characteristics Among Three Seral Stages

A total of 318, 320 and 318 snags were sampled in two young, two mature and two old stands, respectively. Percent bark remaining on the snag, bark condition, snag height and stage of structural decay were the variables most important for the separation observed between snags in young stand versus those in mature and old stands on canonical axis A (Table 2.2; $F=183.21$, $df=12, 1870$, $p<0.001$). In mature and old stands, the percent remaining bark was most often 80 to 100 % (95 % and 84 %) whereas only 19 % of snags in young stands had 80 to 100 % remaining bark. In young stands, it was more common for a snag to have 0 to 20 % remaining bark (43 %). The height of snags in young stands (5.0 ± 4.0 m SD; range=2.0 to 41.0 m) stood apart from the similar heights of snags in old (11.1 ± 8.0; range=2.2 to 31.0 m) and mature (11.2 ± 5.5 m; range= 2.0 to 20.0 m) stands. Young stand snags were classified as structural decay stage 5 (55 %) almost three times as often as snags in mature stands (19 %). Snags in old stands were most often categorized as stage 5 (38 %) and those in mature stands as stage 3 (32 %). Figure 2.4 shows that snags in young stands span a broad range of characteristics; however little overlap in snag characteristics occurs between young stand snags versus mature and old stand snags for these characteristics.

Table 2.2. Structural coefficients of variables for distinguishing among characteristics of snags in young, mature and old stands based on the correlation of the original variables to the canonical functions. This analysis included all snags with and without cavities.

Variable	Correlation to Canonical Function A	Correlation to Canonical Function B
Percent Bark	0.94	0.053
Condition of Bark	0.82	- 0.21
Snag Height	0.54	0.18
Structural Decay	-0.49	0.04
Snag Diameter	-0.19	0.95
Cavity Presence	-0.08	0.27

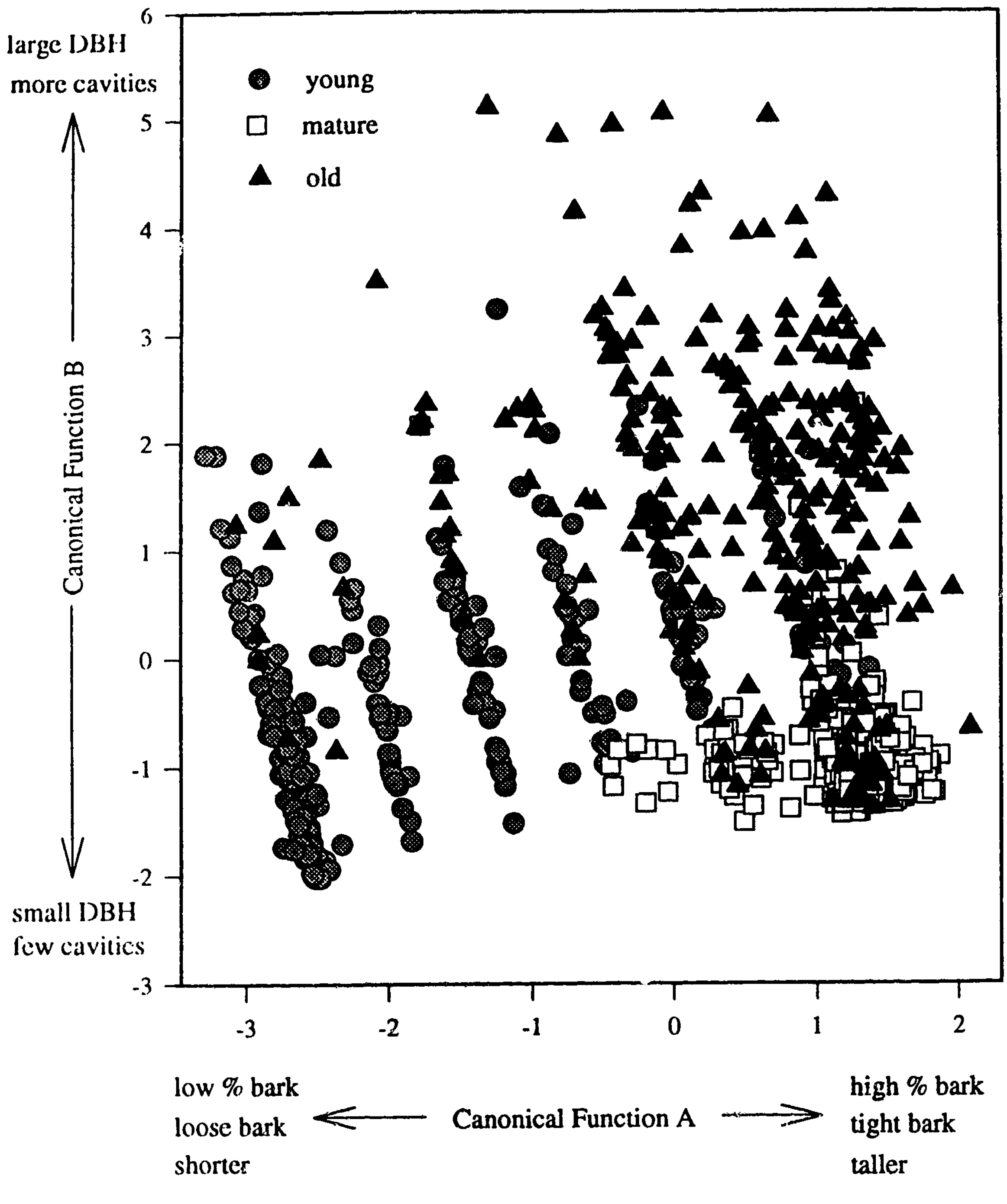

Figure 2.4. The separation observed among characteristics of snags in young, mature and old stands of aspen mixedwood forest. Data points were based on canonical variate scores.

On canonical axis B, snag diameter and presence of a cavity were the most important variables for distinguishing between old stands versus young and mature stands (Table 2.2; canonical discriminant function analysis; F=174.67, df=14, 1868, $p<0.001$). In old stands, snag diameter (32.4 ± 11.5 cm; range=10.0 to 65.0 cm) was twice as large as snag diameter in mature stands (13.2 ± 4.0 cm; range=10.0 to 42.5 cm) and 50 % larger than snags found in young stands (21.4 ± 7.1 cm; range=10.1 to 48.8 cm). Snags in old stands (13 %) had a cavity present almost twice as often as snags in young stands (7 %). It was rare for a snag in mature stands to have a cavity (< 1 %; Figure 2.5). The old stand snags almost completely encompass the range of characteristics found in young and mature stand snags. For the characteristics represented by canonical function B, mature and young stand snags overlap almost completely.

Differences in Characteristics of Snags With and Without Cavities

Of 956 snags sampled, 65 had at least one cavity. Snag diameter and height were the most important variables for distinguishing between snags with and without cavities (Table 2.3; canonical discriminant function analysis; F=24.01, df=5, 937, $p<0.001$). Snags with cavities were taller (13.3 ± 11.1 m) and had a larger diameter (36.6 ± 8.5 cm; Figure 2.5) than snags without cavities (height=8.7 ± 6.5 cm; DBH=21.4 ± 10.7 cm).

Table 2.3. The relative importance of variables for distinguishing between characteristics of snags with cavities and snags without cavities based on the correlation of the original variables to the canonical function.

Variable	Correlation to the Canonical Function
Snag Diameter	0.91
Snag Height	0.40
Structural Decay	-0.14
Percent Bark	-0.13
Bark Condition	-0.12

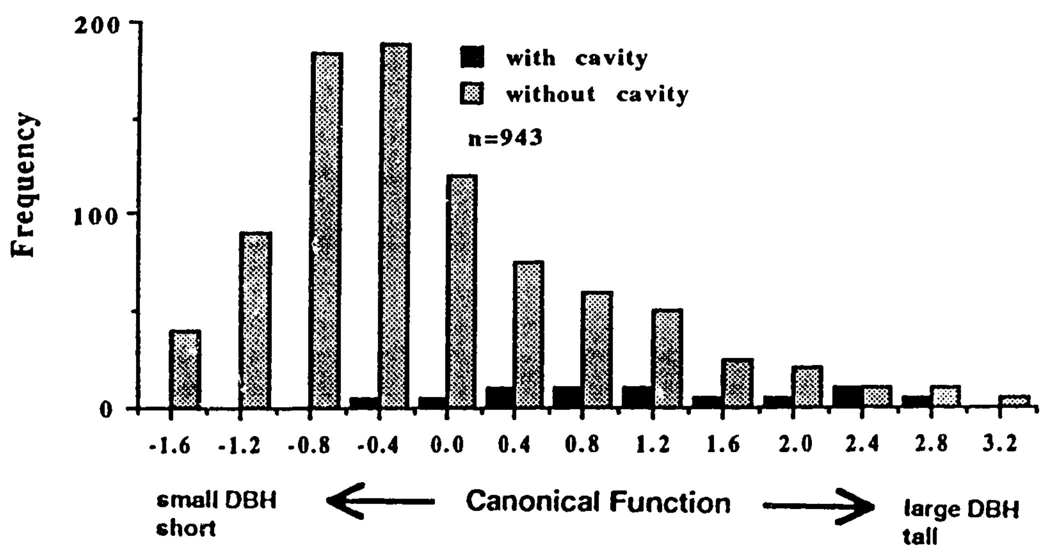

Figure 2.5. The separation observed between characteristics of snags with cavities and snags without cavities in all three stand ages.

Selection of Snag and Tree Characteristics

Selection of Snags versus Live Trees

Although flying squirrels used snags with cavities (n=45) only slightly more than live trees with cavities (n=33; see *Den Tree Characteristics*), selection for snags over live trees occurred since the expected usage, based on relative densities of snags and live trees with cavities, was 32.5 and 45.5, respectively (goodness of fit test; χ^2=8.19, df=1, p<0.005).

Selection of Snag Characteristics

Characteristics of 45 den snags and 55 unused snags with cavities were measured in all three stand ages. Percent bark remaining on the snag and stage of structural decay were the most important variables for distinguishing between used and available snags, (Table 2.4; canonical discriminant function analysis; F=1.46, df=5, 96, p=0.21), but no significant difference was found between the means of these two groups (Figure 2.6). Den snags tended to have higher percent remaining bark and to be in a more advanced stage of decay.

Table 2.4. The relative importance of variables for distinguishing between characteristics of flying squirrel den snags and available snags with cavities based on the correlation of the original variables to the canonical functions.

Variable	Correlation to the Canonical Function
Percent Bark	0.69
Structural Decay	0.21
Snag Diameter	-0.058
Snag Height	0.036
Bark Condition	0.0058

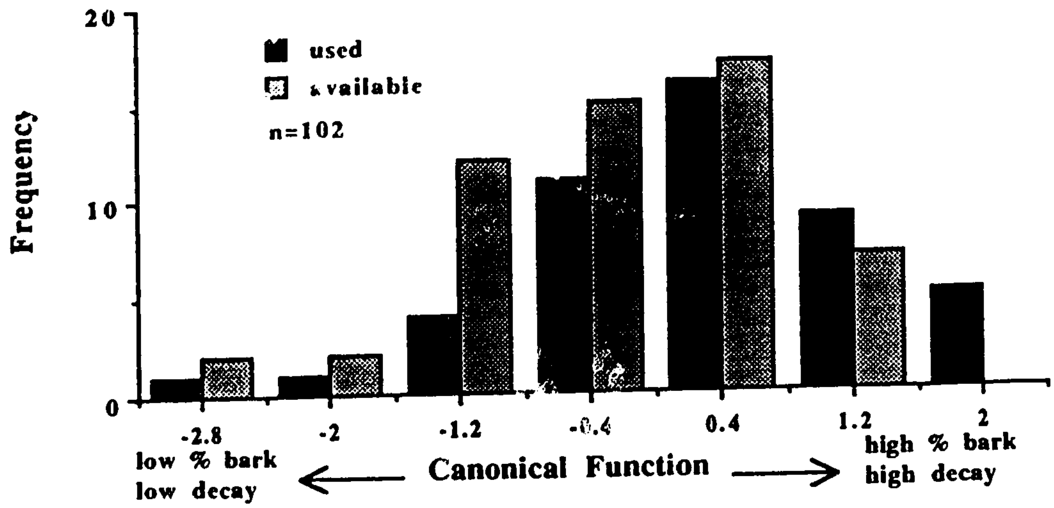

Figure 2.6. The separation observed between characteristics of snags used by flying squirrels and available snags with cavities in all three age classes.

Selection for Live Tree Characteristics

Of 462 available live trees sampled in all three stand ages, only eight had cavities. One cavity was found in each of the young and mature age classes and six were found in the old age class. Because of the low sample size, analysis of characteristics for used versus available live trees with cavities was not done.

Characteristics and Selection of Cavities

Characteristics of Cavities in Three Seral Stages

With equal sampling effort among stand ages, the characteristics of 36 cavities were measured in young stands, ten in mature stands and 103 in old stands. Average cavity height was highest in old stands (13.9 ± 5.3 m SD; range 0.0 to 22.2 m) and very similar between young (5.0 ± 2.8 m; range=0.0 to 11.7 m) and mature (5.3 ± 2.0 m; range=3.3 to 6.1 m). In mature stands, excavated cavities were more common (80 %) than natural cavities (20 %). Excavated cavities were also common in young (69 %) and old stands (54 %), but relatively more natural cavities were found in these age classes. Cavity entrance size was more often sapsucker sized than pileated size in mature stands (90 %)

and old (85 %). In young stands 67 % of cavities were pileated sized. In old stands, as in young stands, the number of cavities on a tree or snag was usually one (44 % and 39 %, respectively) or two (42 % and 32 %, respectively). The number of cavities on a tree or snag in mature stands tended to be one (32 %) or three (39 %) on the tree or snag.

Selection for Cavity Characteristics

A single cavity on a tree and large cavity entrances were the variables that accounted for the differences observed between used and available cavities (Table 2.5; canonical discriminant function analysis; F=2.46, df=5, 212, p=0.034), but the range of characteristics of these two groups overlapped almost completely (Figure 2.7).

Table 2.5. The relative importance of variables for distinguishing between characteristics of used and available cavities based on the correlation of the original variables to the canonical function.

Variable	Correlation to the Canonical Function
Number of Cavities	0.90
Entrance Size	-0.39
Cavity Direction	-0.20
Cavity Type	-0.19
Cavity Height	0.049

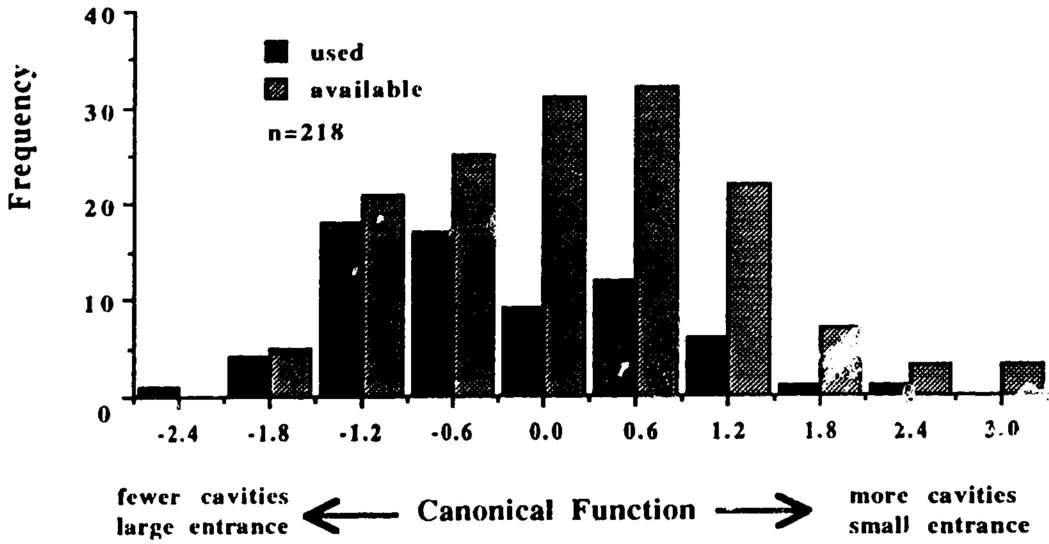

Figure 2.7. The separation observed between characteristics of cavities used by flying squirrels and available cavities in three stand ages.

Flying Squirrel Abundance

Trap nights totaled 2,592 divided equally among four young, four mature and four old stands in 1993. A total of ten squirrels were captured: three in the young stands, none in mature stands and seven in the old stands. Capture rates were 2.0 times higher in old stands than young stands and no squirrels were captured in mature stands (Figure 2.13; Kruskal-Wallis with tied ranks; $H=8.16$, $df=2$, $p<0.005$). Differences occurred between old and mature stands (nonparametric Tukey-type comparison; $Q_{0.05,3}=2.85$), but not between young and mature stands ($Q_{0.05,3}=1.58$), nor between young and old stands ($Q_{0.05,3}=1.27$).

In 1994, trap nights totaled 3,888 divided equally among two young, two mature and two old stands. Nine squirrels were captured with one capture in both the young and mature stands and seven were captured in the old stands. Capture rates were 7.0 times higher in old stands than young and mature stands. Although the pattern of abundance is similar in both years of study, the differences among stand ages are not significant in 1994 (Figure 2.13; H=3.65, df=2, p>0.10). The smaller sample size in 1994, two instead of four stand age replicates, likely reduces the power of the statistical test to detect any differences in abundance among age classes.

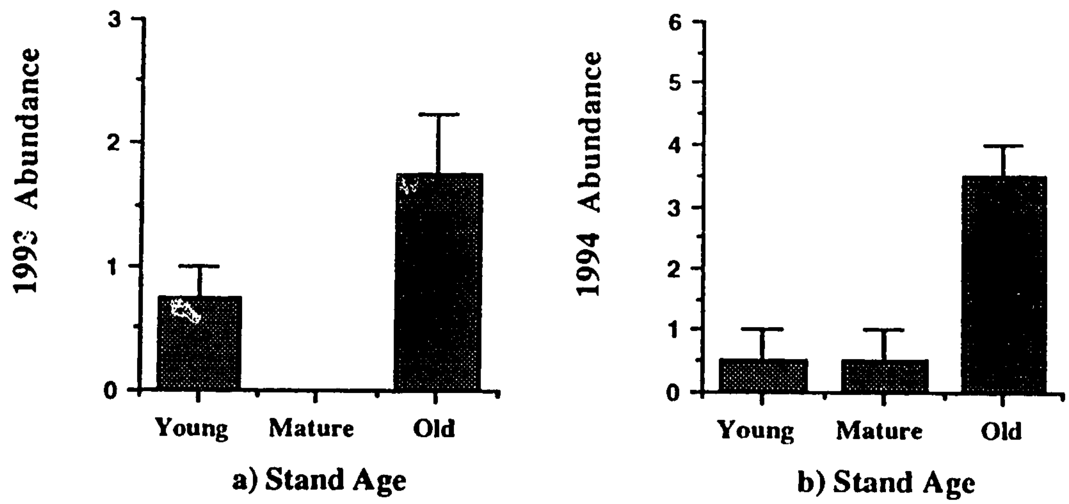

Figure 2.8. The average relative abundance of flying squirrels in young, mature and old stands in a) 1993 and b) 1994.

Discussion

I) Den Tree and Cavity Selection

Northern flying squirrels were found mainly in cavities and occasionally in stick nests, but appear to be incapable of constructing either. Thus, selection for most tree characteristics likely was by the primary excavator or stick nest builder, or the natural processes that create cavities. Primary cavity excavators present in deciduous mixedwood forests include yellow-bellied sapsuckers, downy and hairy woodpeckers, northern flickers and pileated woodpeckers (Schiek and Nietfield 1995). Flying squirrels may select certain trees or snags, but only given that a cavity or stick nest is present. Therefore, only those trees and snags with cavities or stick nests were considered to be available to the flying squirrel. It is within this context that selection by flying squirrels for specific tree characteristics was examined. Since cavities occur naturally in tall, large diameter trees and snags, it is important to consider these factors when attempting to implement proper management techniques.

Flying squirrels selected snags with cavities over live trees with cavities, but selection did not occur for specific snag characteristics. The location of a den cavity, in so far as the tree structure itself, appears to be important to the flying squirrel only in terms of whether or not the tree is live or dead. But, there are some obvious features that differentiate snags from live trees; some which would seem to favor live trees as den sites. The sound structure of live trees would enable them to withstand winds and leaf canopy may provide further shelter and concealment. However, snags are more rotted than live trees. Given this, there may be more potential for larger cavities, or cavities and cavity entrances which flying squirrels could enhance in size on their own. In this and other studies (Cowan 1936; Muul 1974), thin strips of wood were used as nesting material in snags; therefore flying squirrels seem capable of enlarging cavities. A larger cavity may provide the space required for sufficient nesting material, particularly during low temperatures. For northern flying squirrels occupying nest boxes located in coastal British Columbia, Harestad (1990) calculated an average volume of nesting material to be 4373 ± 206 SE cm^3. Further study would be required to determine if flying squirrels select snags because their cavities are larger or can be enlarged.

Selection did occur in terms of cavity characteristics. Flying squirrels strongly selected den cavities where only one cavity was present on the tree or snag. This may ensure that the den tree or snag is used exclusively by the flying squirrel or perhaps predators are more likely to forage on trees with a greater number of cavities. Although no studies have documented a relationship between predation rate and number of cavities, some studies have shown that predator success is decreased by an increased number of potential nest sites (Bowman and Harris 1980; Martin 1993; Badyaev 1995). However, it is not known predation is a significant factor for northern flying squirrels.

Flying squirrels also selected cavities that had large openings. Selection for relatively large entrances is contrary to a study in Georgia (Loeb 1993) in which southern flying squirrels were found to select smaller cavity entrance sizes. However, this apparent difference in selection may be due to differences in the availability of cavity entrance sizes in these different areas. In central Georgia, the average size of cavity entrances used by flying squirrels was 10.2 x 7.2 cm and the average size of available cavities was 12.5 x 8.8 cm. In my study, the entrance size selected was 11 x 6 cm compared to 6 x 4 cm for the small entrance size. The entrance size selected for in each study was very similar. This may indicate that flying squirrels select a specific cavity entrance size rather than the smallest they can find. Thus, previous explanations for selection of smaller cavity entrance sizes may be incomplete. For example, if cavities with small entrances provide protection from predators while reducing competion for den trees from larger cavity users (Bendel and Gates 1987), then flying squirrels should select cavities with the smallest entrances available that they can use, thus maximizing protection from predators and reducing competition from larger cavity users. It could be that a smaller more aggressive animal excludes flying squirrels from using cavities with the smallest entrances available to them. Or, cavity entrance size could indicate a smaller cavity, which may not contain enough room for bedding material needed for insulation.

II) Characteristics of Snags in Three Seral Stages

There were several main differences in snag characteristics among the three age classes. Snags in young stands tended to be short with an intermediate diameter and highly decayed with low percent remaining, loose bark. In mature stands, snags were tall, moderately decayed with a small diameter and high percent remaining bark that was tight on the snag. Old stand snags were tall and had a large diameter, high percent remaining bark that was tight on the snag and a greater likelihood of having a cavity.

Characteristics of snags in this study varied from previous studies examining the relationship between snag characteristics and stand age. However, only the broadest comparisons can be made as few studies have described specific characteristics of individual snags as they vary among stand ages. Several studies (Cline *et al.* 1980; Mannon and Meslow 1984; Rosenberg *et al.* 1988) found increasing densities of snags with stand age in coniferous forests. In my study, snag densities were highest in mature stands followed by old and young stands. These differences may be related to differences in development and retention of remnant structures in coniferous habitats as compared to deciduous habitats. Because decay occurs more slowly in conifer stands than deciduous stands (Tyrrell and Crow 1994), one might expect longer retention of snags and perhaps greater accumulation of snags with time.

Similar to this study, Rosenberg *et al.* (1988) found cavities to be more common in large diameter trees, but again our data were at odds as he found snag diameter to increase with stand age while in my study, snag diameter was greatest in old stands followed by young stands and finally mature stands. Differences in the origin of snags might explain these results. Numerous remnant snags from a previous stand would inflate the average diameter of snags in young regenerating stands if the previous stand contained large diameter trees and snags, and these tree structures escaped fire. A study with a larger sample size of stands within age classes, and thus presumably greater variation in stand origin regarding fire intensity and pre-disturbance stand age, would likely expose the natural variation of remnant structures for stands within age classes.

Likely, most of the dissimilarities in results among studies are due to differences in stand ages and habitat types. Unfortunately, what is often overlooked in studies examining the relationship between snags and the species that use them are the detailed characteristics of snags. The results of my study demonstrate clearly that a snag is not just a snag, but rather a dynamic structure whose characteristics can differ considerably among stand ages. These differences are not easily determined by stand age or snag density, but studies use or dismiss associations based on correlations of snag density with species abundance without measuring detailed characteristics of snags (eg: Schreiber and Decalesta 1992; Westworth and Telfer 1994).

Important assumptions are also often made about the effects of snag densities on animal abundance and on habitat selection. For example, in a study on southern flying squirrels, Fridell and Litvaitis (1991) suggested that female squirrels moved into areas with a greater abundance of potential den trees. It was assumed that the availability of potential den trees was reflected by the abundance of snags, regardless of their characteristics. From my study, it is obvious that snag abundance is not a reliable index of den tree availability. If it were, I would expect to find relatively more suitable den trees, and perhaps flying squirrels, in mature stands. This was not the case. Little confidence should be put into studies that simply examine densities of snags without regard for their characteristics as any relationship to a species abundance and distribution may well be spurious.

III) Abundance of Flying Squirrels in Three Stand Ages

There were several main differences in characteristics of snags in the three age classes: percent bark, condition of bark, snag height, stage of structural decay and snag diameter. If this examination focuses on those characteristics that were also important for separating snags that had cavities from those that did not, that is, mainly diameter and, to a lesser degree height, we can begin to speculate on the paucity of flying squirrels in young and mature stands compared to old stands. The main characteristic separating mature stand snags from old stand snags was small diameter. Although there were a great many snags in mature stands, few had any potential to contain a cavity. Height, although not the most important characteristic, was one that accounted for differences observed between young and old stand snags. Again, there was less potential for a snag to have a cavity in young stands than in old stands.

Although live trees with cavities contributed considerably to the overall density of cavities, particularly in mature stands, live trees with cavities were not selected for. Because selected characteristics likely impart survival or reproductive benefits (Nilsson 1984; Martin and Roper 1988; Kelly 1993), the contribution of live tree cavities to den availability may not be as valuable to the flying squirrel as that of cavities in snags. This may account for the low relative abundance of flying squirrels in mature stands despite higher overall densities of cavities than in young stands. However, flying squirrels do use cavities in live trees nearly as often as snags; therefore, regardless of their relative value as a den site, live trees are obviously an important resource in aspen mixedwood stands.

Given the associative nature of this research, further study on factors limiting flying squirrel abundance is recommended. Habitats with a relatively high abundance of flying squirrels, such as old stands, would be a good place to begin research addressing the limiting factors of flying squirrel abundance. Such experiments might involve removal of snags containing cavities with selected characteristics while monitoring any changes in squirrel abundance.

IV) Management Recommendations

Although current ideas on forestry tend towards maintaining harvested stands as they would appear in a fire regenerated forest (DesGranges and Rondeau 1992; Thompson 1992), this practice may be insufficient to maintain abundance of cavity using species in a managed forest. With the predicted decrease in the amount of old stands in managed forests, it may be necessary to enhance young stands for cavity using species. Perhaps careful planning is needed to increase the retention of remnant structures with cavities into maturing stands. However, research is needed to determine the ramifications of such a move. Changing the habitat attributes of mature stands might maintain cavity using species, but at the same time might exclude species specialized to mature stand habitat.

Northern flying squirrels select single, large cavity entrances on snags for den sites. Fortunately for flying squirrels, snags are more likely to have a cavity than live trees (present study; Rosenberg *et al.* 1988); therefore it may be easier from a management point of view to maintain snags rather than live trees if the objective is to maintain cavities for secondary cavity users in harvested forests.

Although flying squirrels selected cavities with specific characteristics, it is unreasonable to assume that forest companies could manage specifically for these attributes. However, it is feasible for a forest company to manage for the snag and tree components that would increase the probability that cavities, and cavities with characteristics selected by flying squirrels, would persist in managed forests.

This study focuses on den tree and cavity selection. Ensuring that snags and cavities with selected characteristics are present in harvest regenerated forests in no way guarantees the survival of viable flying squirrel populations, but it is likely a good start. Future research should focus on identifying limiting factors and requirements of the northern flying squirrel.

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Chapter IV.

Conclusion

In this study, I examined the relationship between northern flying squirrels and forest age and forest structure, as well as determined patterns of den use and den selection in aspen mixedwood forests. Although this study did not directly test the effects of clearcut timber harvesting on northern flying squirrels, some conclusions can be drawn from the information that was obtained.

It appears that northern flying squirrels existed at low population densities in aspen mixedwood stands relative to conifer forests. Despite this, conservation of this and other rare species is an integral part of conserving biodiversity in harvest regenerated aspen forests. Until we understand the functions and processes of the forest community and the role each organism plays, it would be prudent to maintain, or at least mimic, what occurs in naturally regenerated forests.

The greatest abundance of flying squirrels was found in old stands of aspen mixedwood forest in one year of study and a similar pattern of abundance was observed in the second year of study. Since harvest strategies target old stands and bring these stands into a 60 to 70 year rotation, we will see a truncation of the age class to mainly mature and young stands (Maser 1994). With a loss in the amount of old stands, we might expect to see a decrease in the abundance of flying squirrels in harvest regenerated hardwood forests at the landscape scale. To minimize this loss, some old stands should be excluded from harvesting. To ensure old stands exist in future forests, some harvested stands should be allowed to reach post-rotation age.

Although squirrels are capable of using den trees with a wide range of characteristics, loss of den trees and cavities with selected characteristics in harvested forests could reduce the availability of dens, which offer the best reproductive or survival benefits, below a critical level. This could have adverse effects on flying squirrel populations. Tall, large diameter snags with a single, large entrance cavity should be maintained at the harvest site to increase the probability that dens with selected characteristics will exist in harvest regenerated forests. Likely, the easiest way to maintain snags with selected characteristics is to maintain a wide variety of snags in the distribution they exist at now.

It appears that northern flying squirrels may be particularly sensitive to present harvest strategies at both the landscape and stand scale. Therefore, conservation of flying squirrel populations should involve forest management at these two scales. This approach would likely apply to conservation of any species and to maintenance of biodiversity in aspen mixedwood boreal forests in general.

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