THE UNIVERSITY OF CALGARY

Habitat Selection by Bats and the Potential Impacts

of Forest Fragmentation on Bat Populations

in Aspen Mixedwood Forests in Northern Alberta

by

Lisa H. Crampton

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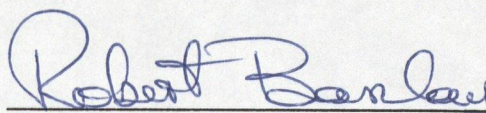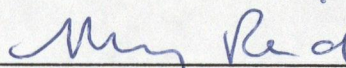
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ABSTRACT

Bats select habitats which provide roosting and foraging sites. In aspen mixedwood forests, these sites likely occur in old stands, and may be threatened by logging. I compared abundance and roosting and foraging behaviour of bats in different forest ages and in logged stands by using mistnets, echolocation call detection and radiotelemetry. In old stands, abundance, foraging and roosting activity of all bats combined and of *Myotis* spp. was greater than in young stands in 1993, and than in either mature and young stands in 1994. Bats selectively roosted in deep cavities in tall aspen trees of low decay class in old stands. Such trees were scarce in other ages. Along edges of some logged sites, bat activity increased, but in unlogged portions of fragmented stands, it did not change. As more roost trees are harvested, I predict that bat abundances will decrease in remnant patches of fragmented stands.

THE UNIVERSITY OF CALGARY

FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Habitat Selection by Bats and the Potential Impacts of Forest Fragmentation on Bat Populations in Aspen Mixedwood Forests in Northern Alberta" submitted by Lisa H. Crampton in partial fulfillment of the requirements for the degree of Master of Science.
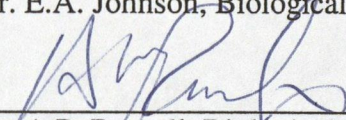
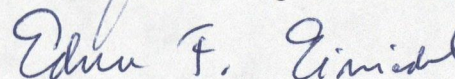Supervisor, Dr. R.M.R. Barclay, Biological
Sciences

Dr. M. Reid, Biological Sciences

Dr. E.A. Johnson, Biological Sciences

Dr. A.P. Russell, Biological Sciences

Dr. E. Einsiedel, General Studies

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Date

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CHAPTER 1

GENERAL INTRODUCTION

Introduction

Animals do not evenly occupy all available habitats within their potential range. Habitats differ in their suitability and therefore in their impact on the reproductive success of animals (Fretwell 1972). Animals, to some degree, are able to select among these different habitats (Fretwell 1972). Habitat selection, because it can influence an animal's fitness (Partridge 1978, Krebs 1985), is an important aspect of animal ecology. It is also a complex issue, as animals must balance many different factors when selecting habitats.

Much work has focused on the choices of habitats made by foraging individuals (e.g. Fretwell 1972, Partridge 1978, Sih 1980, Werner et al. 1983). In theory, an animal should chose a habitat in which it can maximize its net gain, or rate of energy intake (Stephens and Krebs 1986). Quality of food items, including nutrient content (Thompson et al. 1987) may also be important. Animals should choose the habitat with the most abundant and easily obtained food that satisfies their dietary needs. However, competition may diminish the profitability of that habitat compared to less occupied habitats, and thus an individual may choose the latter (Fretwell 1972, Partridge 1978). In this situation, animals are distributed over a variety of habitats in numbers that reflect the differing quality of the habitats, in what is known as the "ideal free distribution" (Fretwell and Lucas 1970, Fretwell 1972). The presence of predators also may limit an animal's range of choices, causing it to avoid some habitats (e.g. Werner et al. 1983, Ferguson et al. 1988). Alternatively, individuals may choose to forage in habitats that offer some refuge from predators.

Other factors may affect habitat selection. The choices of animals also depend on the habitat's provision of appropriate shelter and microclimate for non-foraging activities

such as resting or raising young (Martin 1993), and its suitability for social and reproductive encounters (e.g. in lekking butterflies, Daily et al. 1991). Predation and competition may also influence selection of roosting and mating habitats. The selected habitat may therefore be a compromise among several requirements and risk factors. Animals may make tradeoffs between the quality of a habitat for foraging and its lack of shelter from weather and predators, for example. The relative importance of these features may vary among and within species, as individuals use a variety of habitats for different activities during their lifetime (Hunter 1980). Because of these complexities, often the grounds on which animals select habitats often are poorly understood.

Insectivorous bats are subject to the selective pressures of both their roosting (Kunz 1982) and foraging environments. The choice of habitat by bats during the summer months in the temperate zone may reflect both these pressures; because bats mate during the fall and winter, encountering mates does not affect choice of summer habitats. The availability of suitable roost sites is likely a primary factor in determining their choice of a habitat (Kunz 1982). Bats choose roosts that provide suitable thermal environments, given metabolic and reproductive demands (Hamilton and Barclay 1994), and protection from predators (Fenton et al. 1994). Foraging habitat may be dictated by the morphology and echolocation call type of bats; some bats cannot forage in highly cluttered environments and must forage in more open areas (Aldridge and Rautenbach 1987, Norberg and Rayner 1987). Within this limitation, prey availability is probably the strongest influence on habitat selection (Fenton 1990, Brigham et al. 1992, Saunders and Barclay 1992, de Jong 1994, Kalcounis and Brigham 1995), and competition (Fenton 1990) or predation (Barclay 1989) are likely not as important.

Roost availability may influence foraging habitat (Kunz 1982, Geggie and Fenton 1985, Taylor and Savva 1988), particularly if commuting is costly, but there is some evidence that bats travel long distances from roosts to foraging grounds (e.g. Racey and

Swift 1985, Brigham 1991, de Jong 1994). Unfortunately, few studies examine the relative influences of foraging and roosting requirements on habitat selection by bats. Furthermore, studies of bat habitat use often consider their distribution across very different habitats, but do not look at differences within habitats. For example, several have compared the use of forests (a cluttered environment) by bats to that of other areas, such as meadows and water bodies (e.g. Kunz 1973, Leonard and Fenton 1983; Brigham et al. 1992, de Jong 1994, Kalcounis and Brigham 1995).

Few studies have examined bat habitat selection within forests, despite their use by bats for both roosting and foraging. Some insectivorous bat species forage in and along the edges of forested areas (e.g. Racey and Swift 1985, Krull et al. 1991, de Jong 1994, Kalcounis and Brigham 1995), but others rarely forage in forests (Barclay 1991), perhaps indicating differences in diet and morphology. Bats roost in trees both solitarily and colonially (e.g. Fenton et al. 1993). Bats roost under bark, in cavities, fissures, burned out trees (Taylor and Savva 1988), furrows of bark (Barclay et al. 1988), and hollow trees (Fenton et al. 1993), and hang from branches (Barclay 1984). However, few details are known about the use of forests by bats; the basic roosting requirements and foraging habitats of forest-dwelling bats are yet to be described.

Forests differ in structure and composition with age, location, and disturbance, and thus may vary both in the amount of clutter they present to bats, and in the abundance of suitable roost sites. Bats therefore may prefer certain forests over others. For example, there is evidence that bats prefer older forests to younger ones (Perkins and Cross 1988, Thomas 1988). Disturbances within forests may impact bat habitat selection in that they create openings for foraging (e.g. Crome and Richards 1988), but also remove potential roost trees.

With the increasing rate of forest harvest, an understanding of the basis of habitat selection in forests by bats and other species is important. The effects of this major form

of disturbance on bats are potentially two-fold. First, in the short term, forest fragmentation may create more open areas for foraging, but may cause a loss of roost trees. Second, forest harvest may change the age structure of the forest, by selectively removing older trees, and thus may represent a loss of preferred habitat, especially for roosting. Bats are the major nocturnal predators of flying insects and may play an important role in influencing insect populations, including those of economic pests. In addition, as bats can fly long distances to feed, consume large numbers of insects (Barclay et al. 1991), and have feces rich in nitrogen (Studier et al. 1991), they may affect nutrient dynamics of forest ecosystems. Thus a decline in bat populations in forests may have detrimental consequences for some tree species.

Recently, logging operations commenced in the aspen mixedwood forests of northern Alberta; it is believed that the age distribution of these forests will be truncated by timber harvest (Stelfox 1995). According to range maps, several bat species [little brown bat (*Myotis lucifugus*), northern long-eared bat *(Myotis septentrionalis)*, long-legged bat (*Myotis volans*), silver-haired bat (*Lasionycteris noctivagans*), big brown bat (*Eptesicus fuscus*), hoary bat (*Lasiurus cinereus*), and red bat (*Lasiurus borealis*)] inhabit this region (van Zyll de Jong 1985), yet little is known about their ecology at this northern latitude, and still less about their habitat preferences within the aspen mixedwood forest. It is difficult to predict the potential impacts of logging on the populations of these species. The aims of my study were therefore 1) to determine whether bats are found primarily in certain ages of forest and whether their use of forests for foraging and roosting varies with stand age, and 2) to determine the immediate impact of forest fragmentation on bat abundance, roosting and foraging.

This study is unique in several ways. It is one of the first studies to examine bat habitat selection in forests on the basis of both foraging and roosting criteria, and is the first study of bat habitat selection in the aspen mixedwood forest. This study also

provides the first opportunity to study bat abundance and behaviour in the same stands pre- and post-logging. Other studies have compared activity in neighbouring logged and unlogged sites, and have been unable to separate activity differences due to logging from differences related to varying site characteristics. Furthermore, studies of vegetative structure and composition used the same sites as I did, and I can evaluate my results against these other parameters. Thus I can gain a better understanding of the use bats make of the boreal forest and of general principles of bat habitat selection which I can use to recommend the preservation of forest features essential to bats.

Study Area

I conducted this study in the aspen mixedwood forest to the north-west and north-east of Lac La Biche, Alberta, between 54° and 55° N and 111° and 113° W (Figure 1.1). This forest is dominated by *Populus tremuloides* (trembling aspen), and *Picea glauca* (white spruce) in upland mesic areas. Subdominant species are *Populus balsamifera* (balsam poplar) and *Betula papyrifera* (white birch). Lakes, ponds, streams and muskeg are abundant in the region. *Salix* spp. (willow) is common near water bodies. Low areas with poor drainage are dominated by *Picea mariana* (black spruce) and *Larix laricina* (tamarack). The region's climate is continental, characterised by cold winters, warm summers, and mean annual precipitation of 513.5 mm ± 1106 S.D. (Stelfox 1995).

Stands within the aspen mixedwood forest vary in composition, age, and size (Peterson and Peterson 1992). Some of this variability is due to differences in soil types, and topography (Oliver 1992). Additionally, the primary disturbance factor, fire (Johnson 1992), introduces differences in age and size of stands. The range of ages currently found in the forest is 0-150+ years, with few young stands (Alberta Lands and Forest Services 1994; Figure 1.2).
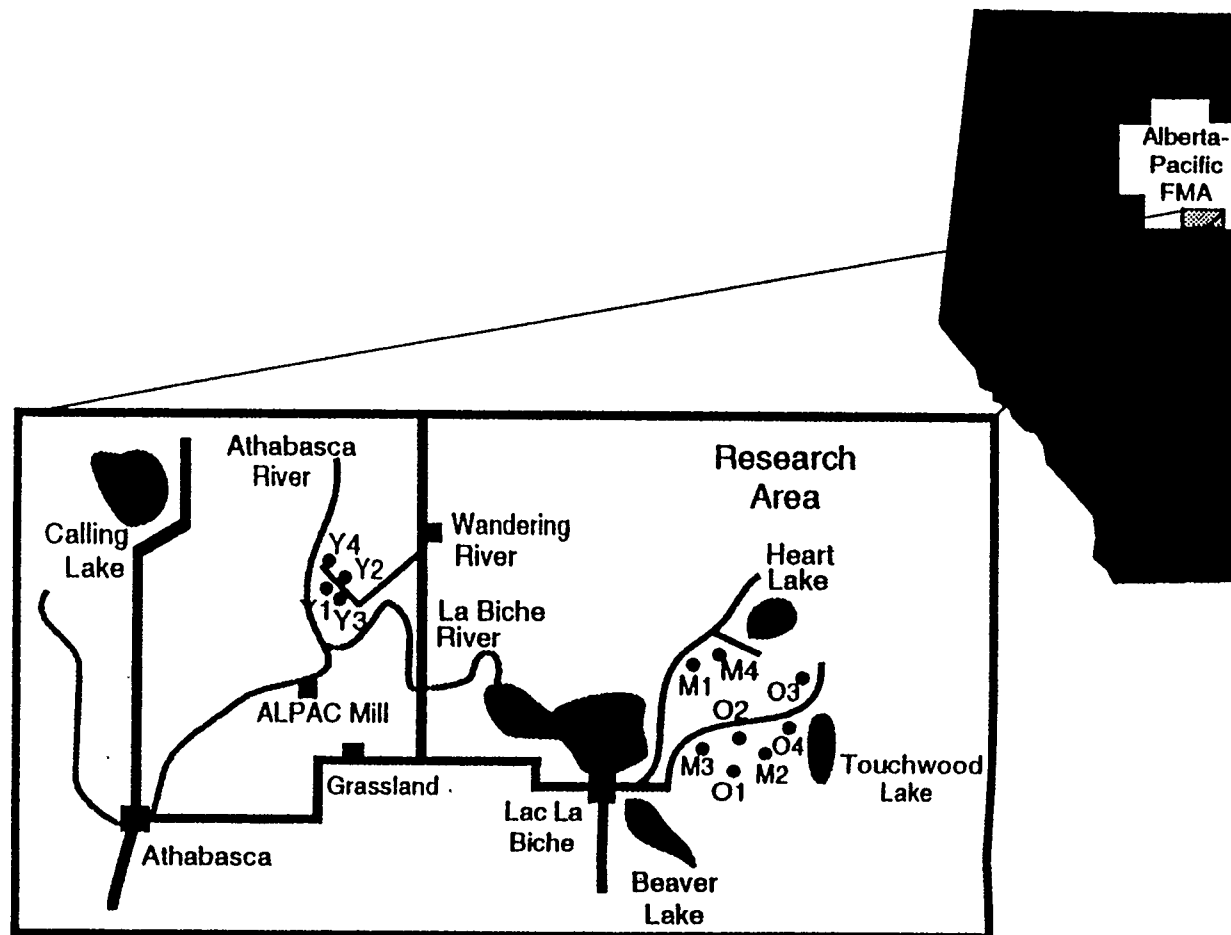
Figure 1.1. Location of forest research stands within the study area in the Alberta Pacific Forest Management Area (FMA) near Lac La Biche, Alberta. Y = young, M = mature and O = old stand (4 stands/age) (from Stelfox 1995).
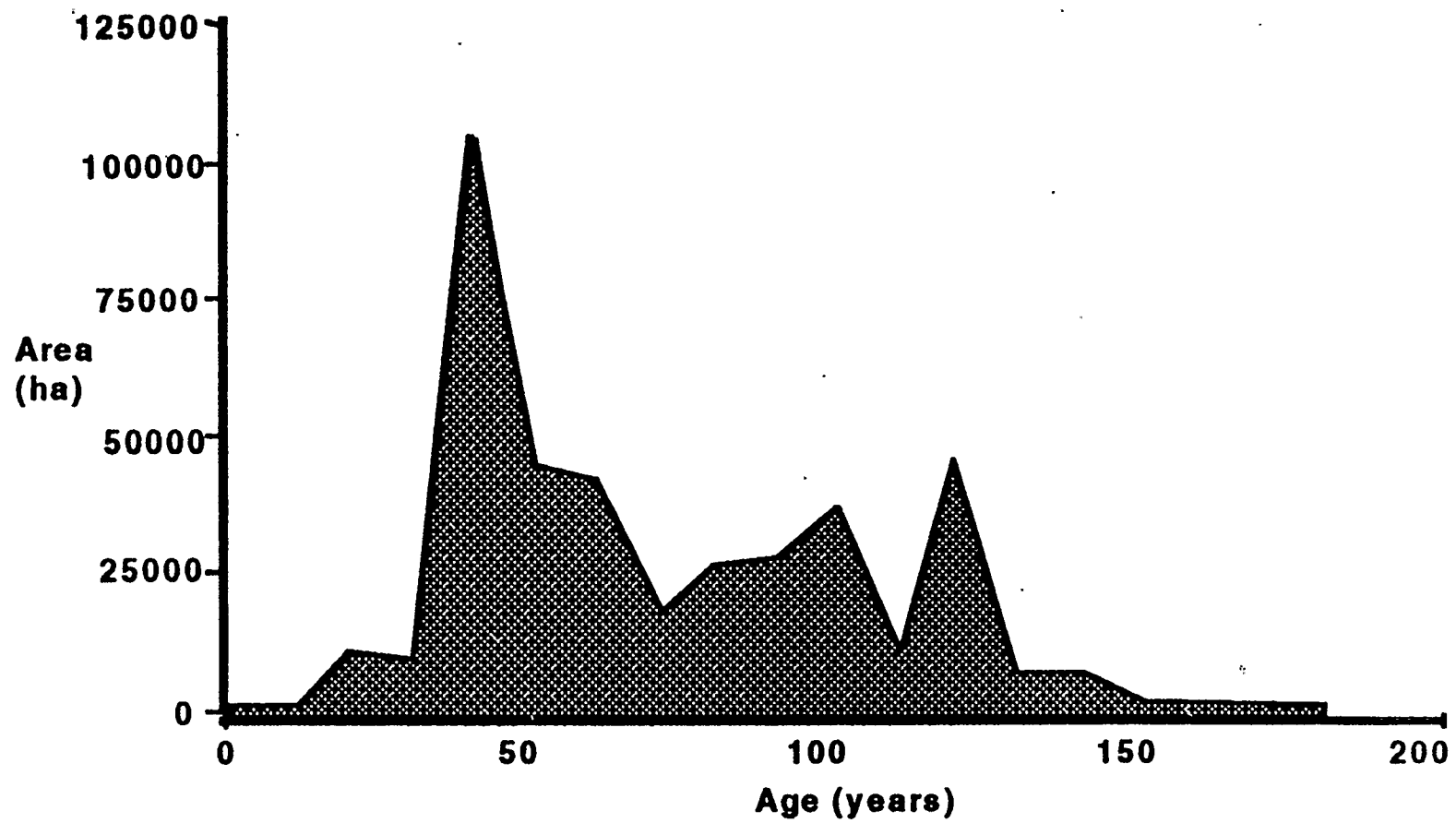
Figure 1.2. Age-class distribution of aspen mixedwood forests in the Alberta Pacific FMA in northeastern Alberta (ages are largely estimated from tree heights; from Stelfox 1995).

Until recently, anthropogenic disturbances in the forest were limited to roads and seismic exploration (Stelfox 1995). Agriculture also infringed on areas of aspen mixedwood forests (Stelfox 1995), but little logging had occurred. Recently, much of the aspen mixedwood forest in Alberta was allocated to timber harvest companies. Current harvest practices, which generally involve clearcutting, impose a 70 year rotation on the forest (Stelfox 1995). Approximately 20% of the forest to be harvested is older than 70 years (Alberta Forestry, Lands and Wildlife 1985). Thus, under current practices, a change in the age structure of the forest is predicted, resulting in old forests to becoming less common (Stelfox 1995).

There is some concern that the predicted change in age structure of the forest will have an impact on the relative abundances of the flora and fauna of the aspen mixedwood forest. Therefore, the Alberta Environmental Centre (AEC) embarked on an assessment of the abundance and diversity of plants, birds and mammals in different aged aspen mixedwood stands, and the potential impacts of timber harvest on the same. My study was part of this larger investigation.

General Methods and Materials

In the summers of 1993 and 1994, I worked in or near twelve pyrogenic stands selected by AEC: four young (20-30 yrs), four mature (50-65 yrs), and four old (> 120 yrs; Table 1.1). AEC located stands of a given age using Phase III AFORISM data (Alberta Forest Service 1985) and verified age by coring. Within each age, AEC then selected four accessible stands of similar structural attributes and of at least 75 ha. All stands were dominated by trembling aspen in the canopy, were mesic, and were of intermediate slope (6-10%). The only anthropogenic disturbances within the stands were seismic lines from oil exploration. Each stand contained six randomly placed sites of 100 m radius (Figure 1.3). Thus the design included four stands of six sites in each age, or 72 sites in total. Site centres, which were indicated by a marker, were at least 150 m from

Table 1.1. Research design, showing aspen mixedwood stands that were fragmented by logging in the winter of 1994.

Stand Age	Stand	Treatment
Young	Y1	Unfragmented
(20-30 yrs)	Y2	Unfragmented
	Y3	Unfragmented
	Y4	Unfragmented
Mature	M1	Unfragmented
(50-65 yrs)	M2	Unfragmented
	M3	Fragmented
	M4	Fragmented
Old	O1	Unfragmented
(> 120 yrs)	O2	Fragmented
	O3	Fragmented
	O4	Unfragmented

a)

stand
perimeter

random
site (100 m
radius)

unsampled
buffer
(100 m
wide)

b)

logged
site

cutblock

edge

forest
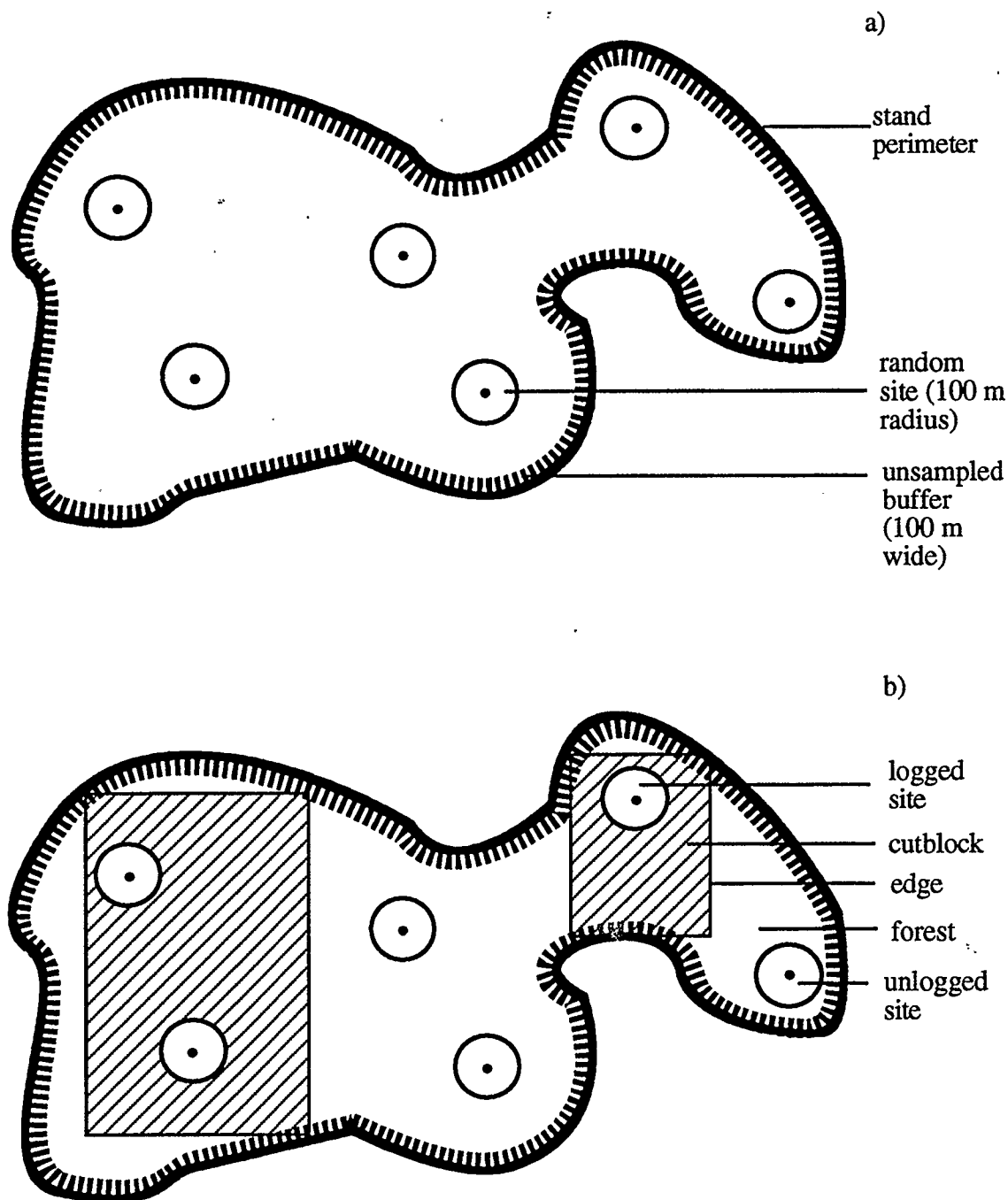
unlogged
site

Figure 1.3. Schematic diagram of 100-m radius sites within research stands: a) sites in unfragmented (control) stands, and b) logged and unlogged sites in fragmented stands, showing also the different habitats sampled in logged areas (cutblock, edge, and forest).

any stand edge, and at least 200 m from neighbouring site centres. I conducted all sampling (except some netting, and radiotracking) in these 100 m radius sites. For more detailed information on the study design see Stelfox (1995).

In 1993, no harvesting had occurred in the area. In this year, I collected data from all stands which I used to compare bat abundance and activity among forest ages. In the winter of 1994, two mature stands and two old stands were fragmented by logging: half the sites in each of these stands (3/6 sites) were incorporated into ~30 ha clearcuts. The remaining mature and old stands, and all the young stands were left intact as controls. The data I collected in the summer of 1994 were then used to assess bat abundance in different ages, and in different treatments. I use the term "logging" to refer to removal of trees at the site level, and the term "fragmentation" to refer to the removal of trees from certain parts of stands. "Unfragmented" refers to the control stands that were left intact in 1994.

In each summer, I sampled one site per night. I randomised the site sampling order across all sites within stand ages, but ensured that I monitored at least one site per stand in every four week period. In 1994, I monitored one logged site each week, alternating between mature and old stands. I did not monitor bat activity in heavy, continuous rain, high winds, or ambient temperatures less than 5°C, as bats were not active under such conditions (see also Rydell 1989a). In each site, I used two primary methods to evaluate bat diversity, abundance and activity: mistnetting and echolocation-call monitoring.

a) Mistnetting: I used one to three nets per night and set nets to approximately 6 m in height no later than 15 min after sunset, for approximately 120-150 min. One net open for 120-150 min counted as one "net-night". I placed nets in gaps within unlogged sites, on cutlines adjacent to unlogged sites, and perpendicular to the edge of logged sites. I recorded the species, sex, age, and reproductive condition (Racey 1988) of captured bats,

and released them at their point of capture.

b) Echolocation-call monitoring: In each site, I identified and counted bat echolocation calls using QMC bat detectors (Summit, 6 Key Hill Rd, Hockley, Birmingham, B18 5NY, U.K.). To differentiate between species groups, I set one detector at 25 kHz [to detect calls of *Lasiurus cinereus*, *Lasionycteris noctivagans*, and *Eptesicus fuscus*, which are distinguishable from one another by frequency and tonal differences (Fenton et al. 1983)], and one detector at 40 kHz (to monitor *Myotis* spp. calls, which are indistinguishable at the species level). For each bat species or species group, I counted the number of echolocation passes (two or more echolocation pulses separated by a one to two second pause from another series; Thomas 1988), during a two hour period beginning 15 min after sunset, which I termed "evening". The number of passes detected per unit time, or bat activity, is an index of the relative use of, or abundance in, each site, and can be compared among sites (Thomas 1988). In each site, I established a transect, and monitored activity at positions along the transect. The details of establishing this transect are discussed in each chapter, as they differed between logged and unlogged sites.

I also used the bat detectors to monitor foraging activity. When bats attack insects, they increase the repetition rate of their echolocation pulses (Fenton and Bell 1979). I recorded the resultant "buzz" as I monitored passes. I compared foraging activity in the two-hour evening period among stands of different ages and treatments.

CHAPTER 2

HABITAT SELECTION BY BATS IN ASPEN MIXEDWOOD STANDS OF DIFFERENT AGES

Introduction

Habitat selection by bats is generally considered to be driven by roosting and foraging requirements (Fenton 1990) and may be the product of interactions between the two (Kunz 1982, Geggie and Fenton 1985, Taylor and Savva 1988). In roost selection, an appropriate thermal environment is important (Racey 1973, Barclay 1982, Hamilton and Barclay 1994), as is protection from predators (Fenton et al. 1994). Colonial species also require roosts that hold numerous individuals; social interactions may benefit individuals of these species in terms of temperature regulation (Roverud and Chappel 1991), information transfer (Wilkinson 1992), and reduced predation risk (Hamilton 1991, Kalcounis and Brigham 1995).

In general, foraging habitat selection appears to depend on echolocation call and wing design, which determine the abilities of bats to deal with physical and perceptual clutter (Aldridge and Rautenbach 1987, Norberg and Rayner 1987, Fenton 1990). Fast flying species, with long range detection systems, are not adapted to forage in cluttered environments (Norberg and Rayner 1987, Barclay and Brigham 1991). Within the range of habitats permitted by the ecomorphology of a species, the distribution of insect prey may be the strongest influence on the habitats used by insectivorous bats (Brigham 1991, Saunders and Barclay 1992, Kalcounis and Brigham 1995). Competition for food may influence partitioning of habitats (Kunz 1973, de Jong 1994), but probably does not restrict bats to certain habitats, as insect prey is not thought to be limiting (Fenton 1990). Predation on active bats is uncommon (Barclay 1989), but may deter bats from using open habitats (Rydell 1986, Krull et al. 1991, de Jong 1994).

Roost availability may also influence foraging habitat (Kunz 1982), leading some bats to forage in poorer quality habitat (Geggie and Fenton 1985), particularly if

commuting is costly. However, if rewards are great, they may outweigh the costs of flying long distances, and bats may take advantage of both prime roosting and foraging habitat. Bats sometimes commute long distances to feed (Racey and Swift 1985, Brigham 1991, Jones et al. 1992, de Jong in press). Bats may balance the costs of commuting against the rewards gained from roosting and foraging in certain habitats (Taylor and Savva 1988); this balance may shift as the costs of commuting or resource availability change. Despite these complex issues in determining the basis of habitat selection, few studies have examined both roost site and foraging habitat selection in bats.

Forests potentially provide both roosting and foraging opportunities to bats, and as such present an environment in which to study the interplay of the two in general habitat selection. The basis of tree roost selection within forests (e.g. Lunney et al. 1988, Taylor and Savva 1988, Vonhof 1995) on one hand, and foraging habitat (e.g. Crome and Richards 1988, Grindal 1995) on the other, have been examined to some degree, but no studies have combined the two. In particular, no studies have examined both roosting and foraging habitat within different forest environments. Forests are not homogenous, but differ in composition and structure (Oliver and Larson 1990, Lee et al. 1995a) and may be perceived by vertebrates as several distinct habitats (Crome and Richards 1988).

The structure and composition of forests, and the resources they provide to animals, may be influenced by age, or time since last disturbance. Several animal species depend on forest features present in certain ages, particularly old forests (Franklin 1988, Rainey et al. 1992, Peterson and Peterson 1992, Thomas 1993, Rudolph and Conner 1994). For example, cavity nesting birds (Mannan et al. 1980, Lundquist and Mariani 1989) and squirrels (Andren and Delin 1994) may select old forests for their abundance of nest trees. Two studies of coniferous systems have associated increased bat abundance with old forests (Perkins and Cross 1988, Thomas 1988). Because forests of different ages may vary in stem density (Thomas et al. 1988), and openness of the canopy (Oliver

and Larson 1990, Lee et al. 1995a), and thus clutter, they may differ in their suitability as foraging habitat for bats. Roosting opportunities may also depend on forest age, as the number of trees of appropriate size (Mannan et al. 1980) and decay, and the number containing cavities (Rosenberg et al. 1988, Healy et al. 1989, Newton 1994) and other shelter for bats, may differ. It is also possible that bat predators and competitors are in greater abundance in some stand ages. Thus bat abundance may vary within forest habitats. Moreover, species may differ in their habitat preferences, based on their ecomorphology (Crome and Richards 1988), and diet (Saunders and Barclay 1992), and thus the bat community may differ among forest ages. By comparing roosting and foraging activity of bats among different ages of forest, we can identify critical elements of habitat selection and contribute to the knowledge of how roost selection and foraging habitat combine to determine general habitat selection. An evaluation of forest age preferences of different bat species allows us to test predictions of habitat selection based on our knowledge of roosting and foraging habitat from other systems.

The aspen mixedwood forest provides an opportunity to study bat preferences for certain forest ages. In these forests, the different ages vary widely in structure and composition. Old forests have lower densities of canopy trees, and more open canopies, hence less clutter, and greater densities of large decaying trees that could potentially provide roosts for bats (Lee et al. 1995a and b). Thus they may have higher bat abundances. Because old-growth aspen is more structurally diverse (Lee et al. 1995a), it may also house a greater diversity of bat species. The aspen mixedwood forest is extensive and remote, and there are few opportunities to forage or roost outside the forest; both behaviours can be studied together in one habitat. Moreover, logging in these forests will change the age structure, reducing the amount of old growth (Stelfox 1995), and an examination of the potential association of bats with old forests is timely.

I tested the hypothesis that bat abundance and diversity in aspen mixedwood forests varies among stand ages, due to differences in forest structure and composition. In particular, I tested two specific predictions:

Prediction 1: The diversity and activity of foraging bats is greater in old stands than in young and mature stands, reflecting the more open nature of old stands, and also the greater number of roosting bats.

Prediction 2: Bats do not select roost trees at random but prefer certain characteristics including adequate shelter, large diameter, accessibility and proximity to foraging areas. Therefore, the number of roosting bats is greater in old stands than in other ages due to the greater number of large trees with roost sites. Roosting bats are more abundant in young stands, which contain pyrogenic snags, than in mature stands. Mature stands are too old to retain such snags but too young to have generated many new large snags.

Methods and Materials

Bat diversity, population structure, and relative abundance in stands of different ages

Between 18 May and 22 August, 1993, I sampled bat diversity and relative abundance in 19 sites in young, 23 sites in mature and 23 sites in old stands. Over the same time period in 1994, I sampled 20 sites in young and 12 sites each in mature and old stands. I sampled one site per night, using two primary methods: mistnetting and echolocation call monitoring. The former primarily addressed questions of diversity and population structure, and the second addressed relative abundance, and to some degree, species diversity, in stands of different ages.

a) Mistnetting: I captured bats with monofilament mistnets in canopy/understory gaps of 4 m minimum length within the 100 m radius of site centre, and also on access cutlines (if they were less than 300 m from site centres and within the stand), as discussed in Chapter 1. In 1993, a total of 47, 47, and 52 net-nights were sampled in young, mature

and old stands, respectively. In 1994, these totals were 46, 33 and 36 net-nights, respectively. These data on bat diversity and population structure were supplemented with data collected for bats netted for radio tracking (see below).

b) Echolocation call monitoring: At each site, I monitored bat activity at 25 and 40 kHz (Chapter 1) for the two hour evening period at various positions along a transect. The initial monitoring positions were at potential roost tree(s) (trees with cavities or loose bark which I found during a 45-minute, pre-monitoring examination of the site) within 100 m of site centre. My assistant and I observed the tree(s) for bat emergence. If there were two or more potential roost trees at the site, one observer monitored one frequency at one tree while the other monitored the other frequency at another tree. If there was only one potential roost tree, we monitored both frequencies at it. After 45 min, we monitored both frequencies together for 20 min periods at points 30 m apart along a transect from the roost tree through site centre along the site access trail towards the nearest cutline. At each point, I recorded the ambient temperature and number of bat passes at each frequency. For each site, I thus obtained a measure of bat activity per hour as an index of relative use or abundance (Thomas 1988). Monitoring echolocation activity also gave me a second indication of species diversity in different age stands.

To determine if there were temporal differences in activity through the night among bat species or stand ages, I monitored activity throughout the night at several randomly chosen sites. I divided the night into three two-hour periods: "evening" (Chapter 1), "morning" (beginning two hours and 15 min before sunrise), and "night", a two-hour period between the other two. Near the solstice, this schedule led to continuous monitoring, but at the end of the summer up to 1.5 h of the night, randomly selected, was not monitored. I monitored the same transect stations during each two-hour period. In 1993, I monitored throughout the night at two sites per stand age in different stands. In

1994, I monitored throughout the night at eight sites in old stands, six sites in mature stands, and five sites in young stands.

Relative foraging activity and foraging habitat

In each site, I also monitored foraging buzzes as I monitored passes. I compared foraging activity in the two-hour evening period among stands of different ages. I also evaluated foraging rate, or the ratio of buzzes to passes, in this period, among stand ages to determine if bats were foraging in proportion to their abundance in those habitats (prediction 1). Additionally, I radio-tracked bats for 60–90 minutes following their exit from roost trees (see below) to obtain information about foraging habitat.

Roosting behaviour

In 1994, in addition to capturing bats at sampling sites, I netted bats over large puddles in seismic lines which ran through, or adjacent to, the research stands. For these bats, I recorded the same variables as in the site sampling program. To 16 of these bats, I attached 0.67 g radio-transmitters (Holohil Systems, RR#2, Woodlawn, ON, K0A 3M0) between the scapulae with Skinbond® (Canadian Howmedica, Guelph, ON) non-toxic surgical adhesive (Hamilton and Barclay 1994). I tracked 14 bats to their roost trees using a Lotek receiver (Lotek Engineering Inc., 115 Pony Dr., Newmarket, ON, L3Y 7B5) and a three-element Yagi antenna. Two non-reproductive females were never detected after release. I only tagged bats that weighed greater than 8 g and selected individuals based on the following order: lactating, pregnant, post-lactating and non-reproductive females, and juveniles. These bats were more likely than adult males to remain within detection range and to lead me to colonies. Battery life of the radiotransmitters was three weeks, although transmitters sometimes were shed after one to two weeks.

I tracked each individual over the course of one to two weeks, but did not generally locate her roost tree daily, as I could not pinpoint all the bats concurrently bearing

radiotransmitters in a given afternoon, and bats often moved large distances. I usually located an individual's roost tree every other day, and noted her general position each day. Therefore, for measurements of residency time and distance between roosts, I only used trees for which I could ascertain the date of arrival; I did not use the trees found the night after capture, as I had no way of determining the residency time. I used the maximum number of days an individual could have resided in a given tree, as long as this was a finite value. For example, if an individual was tracked to a new tree, and two days later, she was in a different tree, I would assume residency in the first tree was two days, not one. Thus I erred towards longer residency times. I did not use trees for which there was no approximate date of departure. I marked roost trees on aerial photos and estimated distances between subsequent trees at which bats were located, when I was certain no intermediate roost had been used.

For roost trees, I recorded a number of characteristics including tree species, height (using a clinometer) and diameter at breast height (DBH). I assigned trees to a decay class based on the condition of the top, number of branches, amount of bark and presence of rot (Appendix 1). I took several measurements of tree clutter which also enhanced my assessment of decay class: percent leaf remaining, percent bare trunk (without leaves or branches), canopy class (based on number and size of branches remaining) and canopy depth. Estimates of percent leaf, bark and bare trunk were made by two observers, and the mean taken. Appendix 2 lists all variables measured and used in statistical analyses. I also recorded the roost type, entrance dimensions, and height on the tree. If the roost tree was not within one of our research stands (n=11 trees), I estimated stand age using aerial photos showing stand boundaries, supplemented with visual assessment of characteristics such as: dominant canopy and subcanopy species, height, DBH and canopy heterogeneity of the surrounding vegetation, number of wildlife trees (see p. 20) within 25 m radius and distance to nearest wildlife tree.

At sunset, I observed a roost tree for 45-60 minutes, counted the number of bats which emerged, and noted bat behaviour at the tree. I also monitored the direction, duration, and approximate distance (based on signal strength) of flight by the radiotagged bat using radiotelemetry. After radio-tagged bats left their roost trees, I tracked them for another 20-45 minutes from various locations, for a total of 60-90 minutes of tracking.

I also measured a random sample of wildlife trees, defined as live and dead trees showing any sign of decay (M. Nietfeld, pers. comm.), having a minimum DBH of 10 cm, maximum lean of 45°, minimum height of 1 m, and a scar, hole, crack, or piece of loose bark at least 1x2 cm in entrance size. To obtain this sample I used a T^2 method (Krebs 1989). In each site, I identified points 25 m from site centre at bearings of $0°$, $120°$, and $240°$, and located the nearest wildlife tree within a 25 m radius of the point. I then searched for a second tree in a 25 m radius hemisphere from the first tree, ensuring that I did not search again in the area searched for the first tree. If no trees were found within the 25 m boundary, I did not measure a tree. This method usually generated six random trees/site, although in some young stands it generated only four or five. For each tree, I recorded the same characteristics as for roost trees, except stand characteristics. I compared the features of the roost trees to those of the random wildlife trees to determine whether bats were selecting trees for certain characteristics and if those characteristics were more abundant in stands of certain ages. In this way I could assess whether the availability of "bat" trees in old, mature and young stands is an important determinant of bat abundance and activity (prediction 2). Because high, deep cavities appear only as black spots on the tree, the random sample may underestimate the availability of such potential roosts.

Statistical Analyses

Bat diversity, population structure, and relative abundance in stands of different ages

To determine if there were differences in the number of bats caught in stands of different ages, I compared the actual number of captures in different ages to the expected

number of captures (based on number of net-nights/age) for total bats, *Myotis* spp. and *Lasionycteris noctivagans* (silver-haired bat) using chi-squared tests. "Total bats" refers to all bats captured or detected regardless of species. Because I caught so few bats in the site sampling program, I pooled captures in 1993 and 1994, and analysed these together. I analysed captures from the radiotracking program separately.

I compared the number of total, *Myotis*, and *L. noctivagans* passes detected in different stand ages between the two years using a two-way analysis of variance (ANOVA) with year and stand as main effects. I conducted separate analyses for each age, and each of the two hours of the evening. Although there was no statistical difference between years, reduced sample size in 1994 made it impossible to use statistical models which included year as a main effect in subsequent tests of the effect of age on bat activity. Therefore, I analysed the data for the two years separately. I used a two sample t-test to compare mean monthly temperatures at sunset between the two years.

I also compared the number of total, *Myotis,* and *L. noctivagans* passes in hour 1 (the hour beginning 15 minutes after sunset) to that in hour 2 using an analysis of covariance (ANCOVA) with hour as the main effect and date as a covariate. I discarded date from the final model as it was insignificant. In subsequent analyses, I analysed data for the two hours separately, as in 1994 hour 1 had significantly greater mean total activity (39.9 passes/h) than hour 2 (4.58 passes/h; $F=15.1$; df=1,22; $P < 0.001$). In 1993, a large number of sites had no activity, resulting in a non-normal distribution; therefore, I could not perform this analysis. However, plots of means for hours 1 and 2 suggested a difference in activity, and therefore I again analysed data for the two hours separately.

Because activity in hour 1 and hour 2 in both years was not normally distributed, I proceeded in two stages for each year's data for my assessment of differences in activity among stand ages. First, I considered only whether bats were present (one or more passes detected) or absent (no passes detected) in stands of different ages in hour 1 and in hour 2;

I termed this distinction "occurrence". For 1993 data, I fitted a transformed logistic response function to the proportion of sites per stand in which bats were present (Neter et al. 1985) before performing an ANOVA with age as the main effect (4 stands per age). I then compared activity between different pairs of ages using a t-test on the least squares mean proportion (transformed as above) of sites per stand. I repeated these tests on data for *Myotis* and *L. noctivagans*.

In 1994, due to lower sampling intensity, I used a chi-squared test to evaluate if there were differences among stand ages in the number of sites per stand age in which at least one bat occurred. Based on the 1993 results (see below), I first compared young stands to mature stands. If there was no significant difference, I pooled data from young and mature stands and compared the pooled data to data from old stands. I analysed each hour separately and repeated the procedure on data for *Myotis* and *L. noctivagans*.

In the second stage of analysis, for each year I contrasted total bat activity among ages in hours 1 and 2 for sites in which bats were present. I conducted ANCOVA on log-transformed data with age as a main effect, stand nested within age, and ambient temperature and date as covariates (to control for seasonal effects). Insignificant interactions or covariates (slopes were homogenous) were discarded sequentially from the third order interaction to covariates. I specified a random term for stand. I conducted Tukey's tests and pairwise t-tests to determine which ages differed in mean activity using $\alpha_c = 1-(1-\alpha_F)^{1/3} = 0.017$ as the level of significance (Zar 1984). There were insufficient data to conduct this stage of analysis for *Myotis* and *L. noctivagans*.

I compared bat activity for total, *Myotis*, and *L. noctivagans* during the different periods of the night with a two-way ANOVA on log transformed data with date and period as main effects. Because all-night sampling was limited to a few sites each year, I pooled data for the two years. I analysed data for each forest age separately, and included sites in which no bats were detected.

Relative foraging activity and foraging habitat

To determine if there were differences in foraging activity among ages, I used a chi-squared test to compare the observed number of feeding buzzes to the expected number (based on sampling intensity) among ages. I conducted this test for total, *Myotis* and *L. noctivagans* buzzes in each year. I could not perform statistical tests on foraging rate as the data were too limited.

Roosting behaviour

I evaluated species' differences in selection of roost tree characteristics for all continuous variables (e.g. roost tree height, DBH, distance to canopy) using a nested ANOVA with bat species as the main effect, and individual bat as a nested effect (as some bats roosted in more than one tree). For discrete variables (e.g. tree condition, presence of rot), I qualitatively compared frequency distributions of these variables to see if the two species' preferences were similar. I also compared species selection of rot classes, top condition, and distance to edge with two-tailed Fisher exact tests. There were no clear differences between the species' selection of any characteristic, and thus values for the two species were pooled in subsequent analyses.

Because all roost trees were found in old stands, I compared continuous variables of roost trees and random wildlife trees in old stands using a stepwise discriminant functions analysis (DFA) to determine whether bats were selecting trees with certain characteristics from among available wildlife trees in old stands (assuming that bats did not occupy the latter). For this analysis, I used only the first random tree sampled at each bearing in each of the old sites (three random trees per site). I then conducted a canonical discriminant functions analysis on the same data with the significant variables. I thus obtained a measure of the contribution each variable makes to the discrimination, the total canonical structure coefficient (TCSC). The sign of the TCSC assigns each tree to one of

the two groups as its value for the variable in question increases, as the TCSC indicates the position of that variable along the discriminant axis.

For top condition, presence of rot, edge size, and canopy class, I compared roost to old-stand random wildlife trees with chi-squared tests. I used all old random trees sampled. I used randomisation tests to compare decay class, bark condition, distance from edge and tree species of roost trees to those of random trees. I also used chi-squared tests to compare type of roost in roost trees to that in random trees.

All values are expressed as means ± S.E. unless otherwise stated. Means and S.E.'s for log-transformed activity data were back transformed, resulting in asymmetrical S.E.'s. I used $\alpha=0.05$ as the level of significance unless otherwise stated. For chi-squared tests, Yates' continuity correction was used where appropriate (df=1; Zar 1984).

Results

I confirmed the presence in all stand ages of three species [*L. cinereus* (hoary bat), *L. noctivagans*, and *E. fuscus* (big brown bat)] and one genus (*Myotis*), using echolocation call monitoring. For a given species, relative activity levels was similar between years (Figure 2.1). Most (70-75%) of the echolocation activity (passes/h) was *Myotis* spp., followed by *L. noctivagans*, *E. fuscus*, and *L. cinereus*. I was unable to identify some calls on 25 kHz to species (8% in 1993: n=1061 passes; 2% in 1994: n=1982 passes; n's include detections during all-night sampling).

I caught 30 bats in the site sampling program (293 net-nights over the two years), and 69 bats in the radiotracking program (32 net-nights in 1994; Table 2.1). These captures allowed me to identify two of the species in the *Myotis* spp. group: *M. lucifugus* (little brown bat) and *M. septentrionalis* (northern long-eared bat). Based on range maps (van Zyll de Jong 1985), it is possible that *M. volans* (long-legged bat) exists in the area, but none was caught. *M. lucifugus* dominated captures (80 bats total from all nets in the
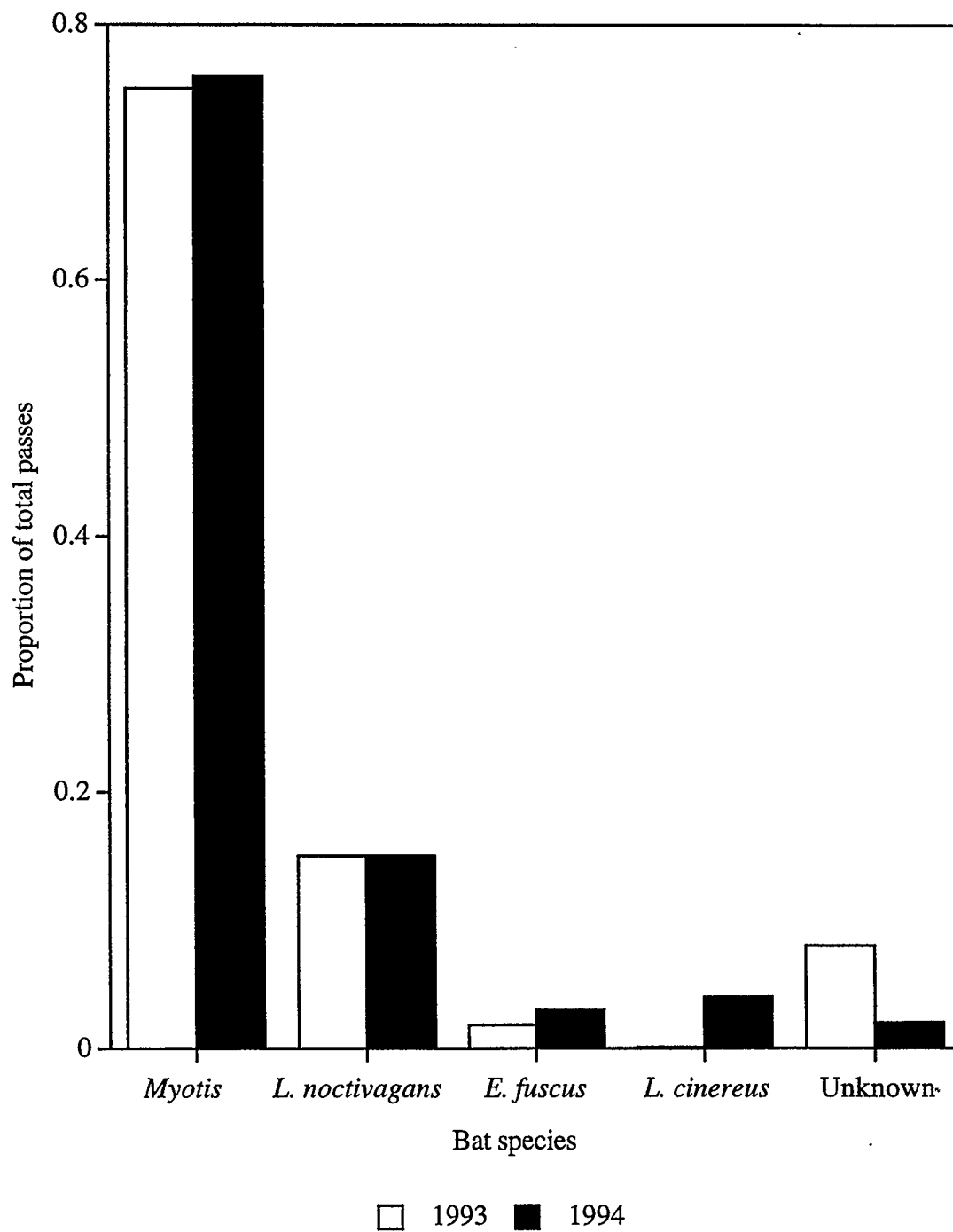
Figure 2.1. Proportion of total passes detected for different bat species in unlogged sites in the aspen mixedwood forest in 1993 (n=1318 passes) and 1994 (n=1982 passes; n in both years includes all-night sampling).

Table 2.1. Number, age and sex of bats caught in aspen mixedwood forests of different ages in 1993 and 1994. S represents the total numbers of bats caught in conjunction with site monitoring in both years; R represents bats caught in conjunction with radiotagging in 1994; the number in parentheses is the number of net-nights (or sampling effort) for each forest.

Species	Age	Sex	Forest Age						Total
			Young		Mature		Old		
			S (91)	R (3)	S (93)	R (11)	S(109)	R (18)	
Myotis lucifugus	Adult	F	0	1	5	0	8	45	59
	Adult	M	0	2	0	1	3	2	8
	Juv.	F	0	1	1	3	5	0	10
	Juv.	M	0	1	0	2	0	0	3
		Total	0	5	6	6	16	47	80
M. septentrionalis	Adult	M	1	0	0	0	0	0	1
Lasionycteris noctivagans	Adult	F	1	0	0	3	0	4	8
	Adult	M	0	0	0	1	0	0	1
	Juv.	F	1	0	3	1	0	0	5
	Juv.	M	0	0	1	1	1	0	3
		Total	2	0	4	6	1	4	17
Lasiurus cinereus	Adult	F	0	0	0	1	0	0	1

M=male
F=female
Juv.=juvenile

two years), followed by *L. noctivagans* (17 bats), and then *M. septentrionalis* and *L. cinereus* (1 bat each). No *E. fuscus* were caught in either year. Adult males, reproductive females, and juveniles of both sexes of *M. lucifugus* and *L. noctivagans* were captured over the two years. The first juvenile *M. lucifugus* was caught on July 18, 1993 and on July 13, 1994. Lactating *M. lucifugus* females were caught as late as August 2, 1993 and July 26, 1994. Reproductive events of *L. noctivagans* appeared to occur approximately a week later than those of *M. lucifugus*.

The total number of passes was greater in 1994 than in 1993 in the first two hours of the night in sites sampled in both years (1111 versus 763 passes). This change was due primarily to increased bat activity in old stands. In old stands, total passes increased from 647 in 1993 to 1076 passes in 1994 and from 69 *L. noctivagans* passes in 1993 to 237 in 1994. However, there was no significant difference in total activity in old stands between years (F=2.21, df=1,10, $P > 0.1$). Total activity in mature and young stands remained low over both summers. Mean monthly temperatures did not differ between the two years, although 1993 generally was colder than 1994, particularly in May (1993=9.5°C, 1994=12.7°C; t =1.69, df=14, $P > 0.05$).

Bat diversity and relative abundance in stands of different ages

Both mistnetting and echolocation call monitoring demonstrated that bats were more abundant in old stands than in younger stands. In both the site sampling and radiotracking programs, I caught *M. lucifugus* and *L. noctivagans* in stands of all ages. However, more· bats were caught in old stands than were expected based on netting effort, whereas the expected number was caught in mature stands, and fewer than expected were caught in young stands (sites: χ^2=6.40, df=2, $P < 0.05$; radio: χ^2=11.51, df=2, $P < 0.005$; Figure 2.2). The same pattern of greater abundance held for *M. lucifugus* (sites: χ^2=14.83, df=2, $P < 0.001$; radio: χ^2=16.06, df=2, $P < 0.001$). *L. noctivagans*, however, was

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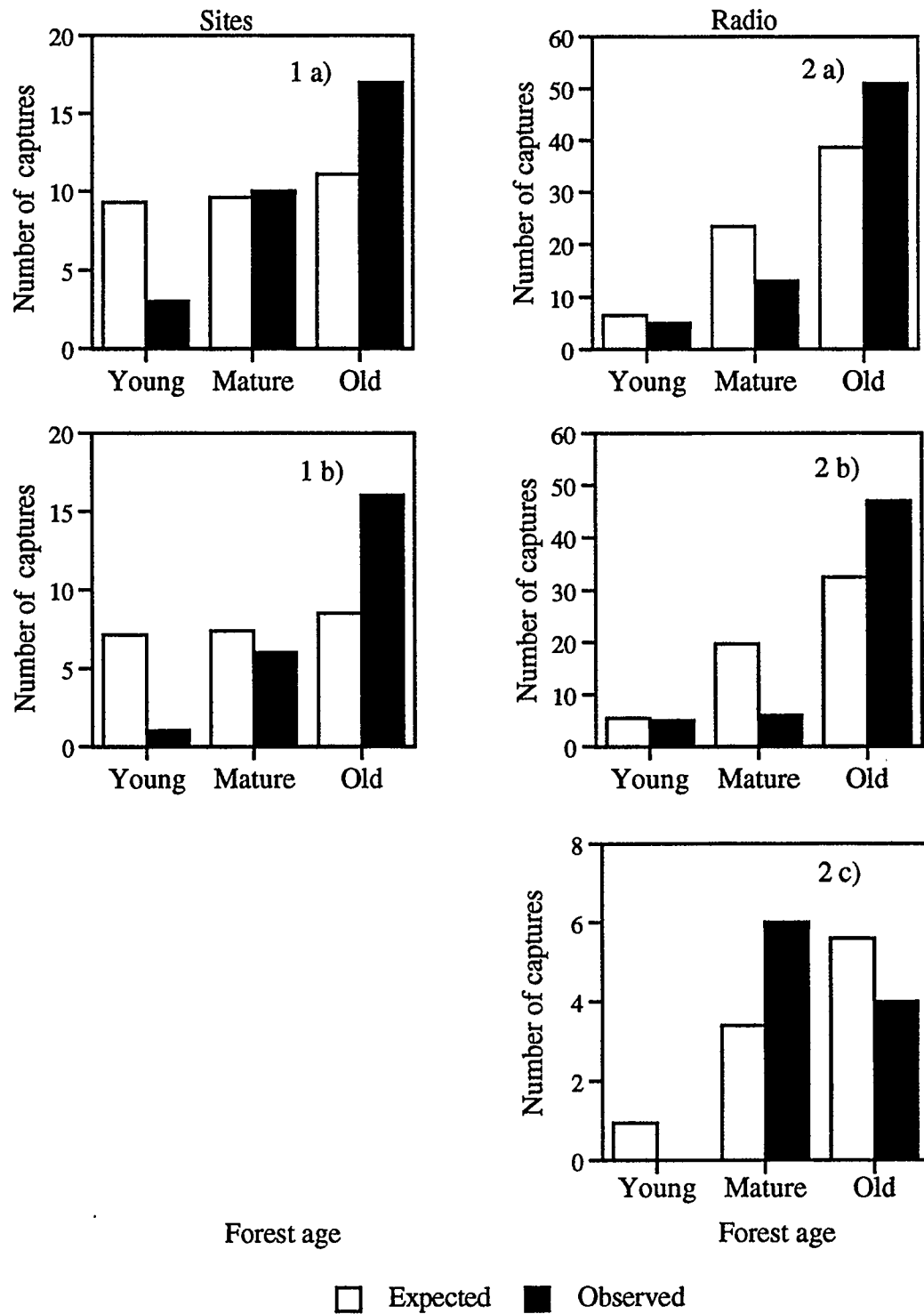
Figure 2.2. Comparison of observed to expected (based on netting effort) number of captures for different species groups in young, mature, and old aspen mixedwood stands. "1" refers to bats caught in site sampling, "2" to those caught in the radiotracking program; a) total, b) *M. lucifugus.*, c) *L. noctivagans*. I caught too few *L. noctivagans* in site sampling to conduct this analysis.

caught at approximately the expected proportions in all ages in the radiotracking program (χ^2=3.4; df=2; $P > 0.05$); too few were caught in site sampling to conduct this analysis.

In both years, relative total abundance of bats (based on echolocation passes) was greater in old stands than in mature or young stands (based only on stands sampled in both years). In 1993, in hour 1, the mean proportion of sites in which at least one bat was detected differed among ages (F=6.64; df=2,9; $P < 0.05$). The proportion of sites in which at least one bat was detected was significantly higher in old stands (0.82) than in young stands (0.39; t =3.3; df=9; $P < 0.01$; Figure 2.3), but did not differ significantly from that of mature stands (0.68; t =1.36; df=9; $P > 0.2$). In hour 2, the proportion of sites with bats in old (0.49) and mature (0.48) stands declined, and there was no difference among ages (young=0.45; F =0.04; df=2,9; $P > 0.9$).

In 1994, there was no significant difference between young and mature stands in the occurrence of bats in either hour (Yates' χ^2=0.01; df=1; $P >0.9$). Therefore, I pooled data for these two stand ages and compared them to old stands. In hour 1, at least one bat was detected in 11/12 (92%) old sites compared to 17/32 (53%) young and mature sites combined, a significant difference (Yates' χ^2=4.1; df=1; $P < 0.05$; Figure 2.4). In hour 2, at least one bat was detected in 11/12 (92%) old sites and in 18/32 (56%) young and mature sites combined; this difference was not quite significant (Yates' χ^2=3.4; df=1; P =0.06).

The pattern of occurrence of *Myotis* spp. in different stand ages was similar to that of total bats (Figures 2.3 and 2.4). In 1993, the mean proportion of sites in which *Myotis* was detected was significantly greater in old stands (0.75) than in young stands (0.21; t =3.3; df=9; $P < 0.01$; α_c=0.017; overall model F=6.0; df=2,9; $P < 0.025$) in hour 1. The mean proportion of sites in mature stands in which *Myotis* occurred (0.33) was slightly higher than in young stands, and did not differ significantly from the proportion in either young or old stands. In hour 2, the mean proportion of sites in old stands in which *Myotis* occurred was lower than that for hour 1, and there was no difference among ages
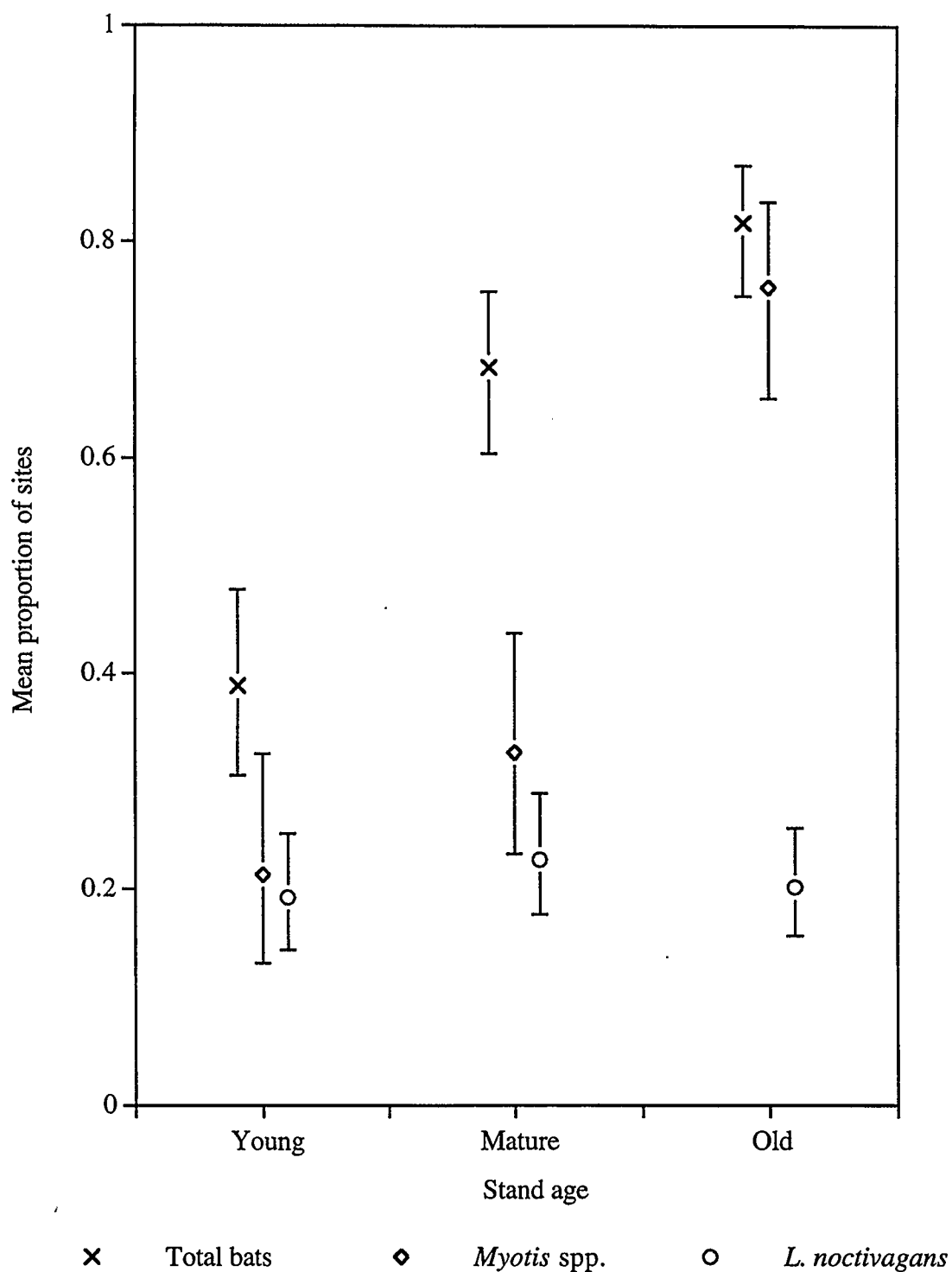
Figure 2.3 . The mean (± S.E.) proportion of sites in aspen mixedwood stands of different ages in which at least one bat was detected in hour 1, 1993. Means and S.E.'s were calculated from log-transformed data, and thus S.E.'s are aymmetrical. n= 4 stands/age, and from 4-6 sites/stand.
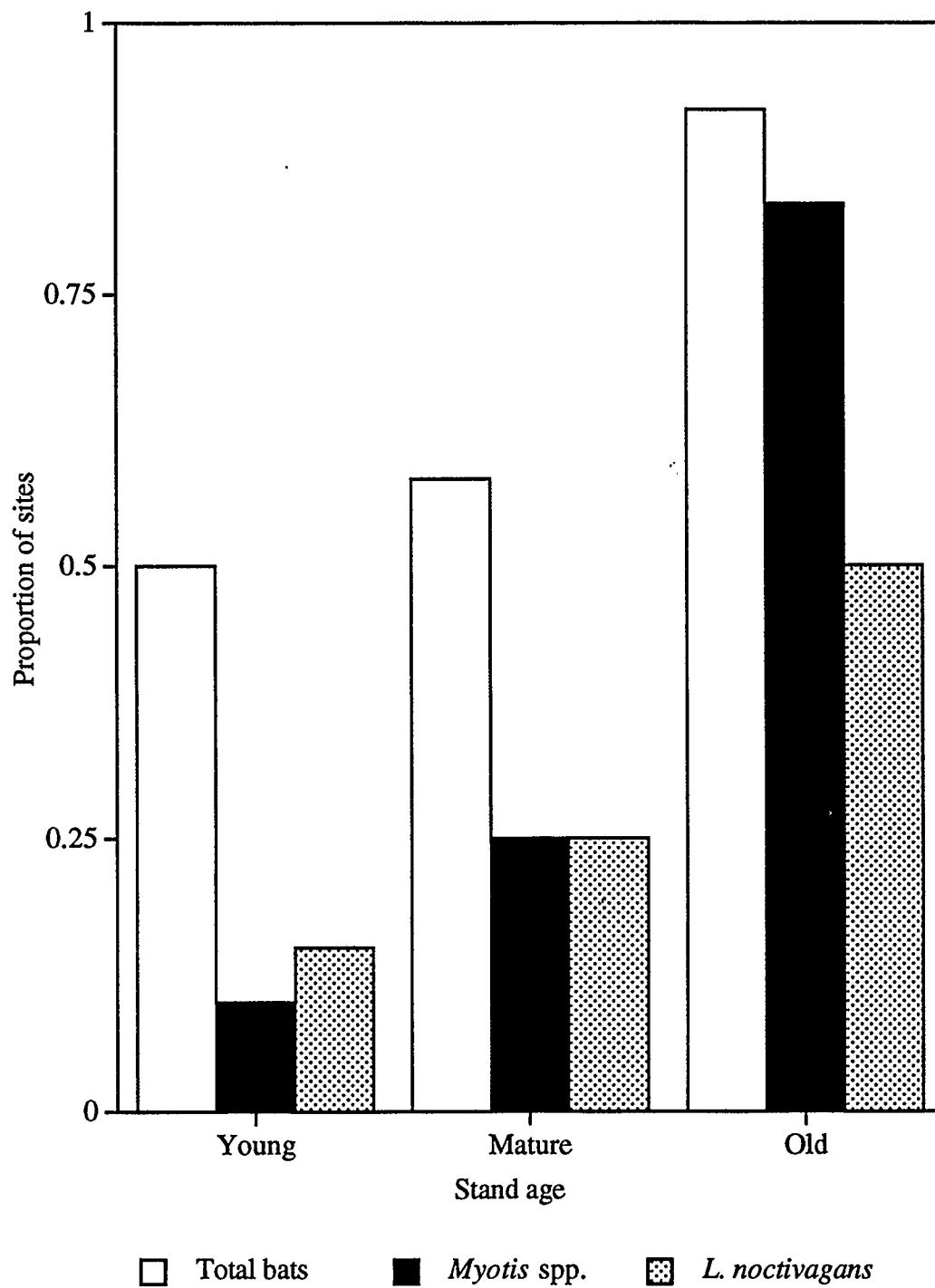
Figure 2.4. The proportion of sites in aspen mixedwood stands of different ages in which at least one bat was detected in hour 1, 1994. Young: n=20, Mature: n=12, Old: n= 12 sites.

(young=0.24; mature=0.28; old=0.32; F=0.3; df=2,9; $P > 0.7$). In 1994, the proportion of sites in old stands 10/12 (83%) in which at least one *Myotis* was present was significantly greater than the proportion of sites in the other ages [5/32 sites (16%); Yates' χ^2=14.92; df=1; $P < 0.001$] in both hours.

The proportion of sites in which at least one *L. noctivagans* was detected was low in all stand ages in both years (Figures 2.3 and 2.4). The mean proportion of sites in which *L. noctivagans* occurred was approximately equal in all stand ages in both hours in 1993 (hour 1: young=0.19; mature=0.23; old=0.20; F=0.1; df=2,9; P=0.90; hour 2: young=0.34; mature=0.35; old=0.25; F=0.4; df=2,9; $P > 0.6$). In 1994, *L. noctivagans* occurred in 6/32 (19%) young and mature sites combined and 6/12 (50%) old sites in hour 1, and 4/32 (12%) young and mature sites combined and 2/12 (17%) old sites in hour 2. These differences were not significant (hour 1: Yates' χ^2=2.87; df=1; $P > 0.05$; hour 2: Yates' χ^2=0.0; df=1; $P > 0.9$).

In 1993, when bats were present, old stands appeared to have greater total bat activity, particularly in hour 1, but the overall ANOVA model was not significant (F=1.5; df=11,32; $P > 0.1$; Figure 2.5). Mean total activity in 1993 was 10.1 passes/h in old, 3.2 passes/h in mature, and 2.3 passes/h in young stands. In 1994, activity differed significantly among stand ages (F=39.9; df=2,4; $P < 0.005$). Old stands had significantly higher mean total passes/h (55.0) than either young (1.6; t=7.97; df=20; $P < 0.001$) or mature stands (2.1; t = 7.05; df=20; $P < 0.001$) in hour 1. There were no significant differences among ages in hour 2 in either year. In hour 2, 1993, mean activities of 2.3, 4.6, and 7.1 passes/h were detected in young, mature, and old stands, respectively. In hour 2, 1994, these values were 1.9, 2.7, and 5.3 passes/h, respectively. There were no differences among stands within ages in either year or either hour (e.g. hour 1, 1994: F = 1.23; df=5,20; $P > 0.3$). There were insufficient data to evaluate differences in *Myotis* or *L. noctivagans* activity among stand ages in either hour or year.
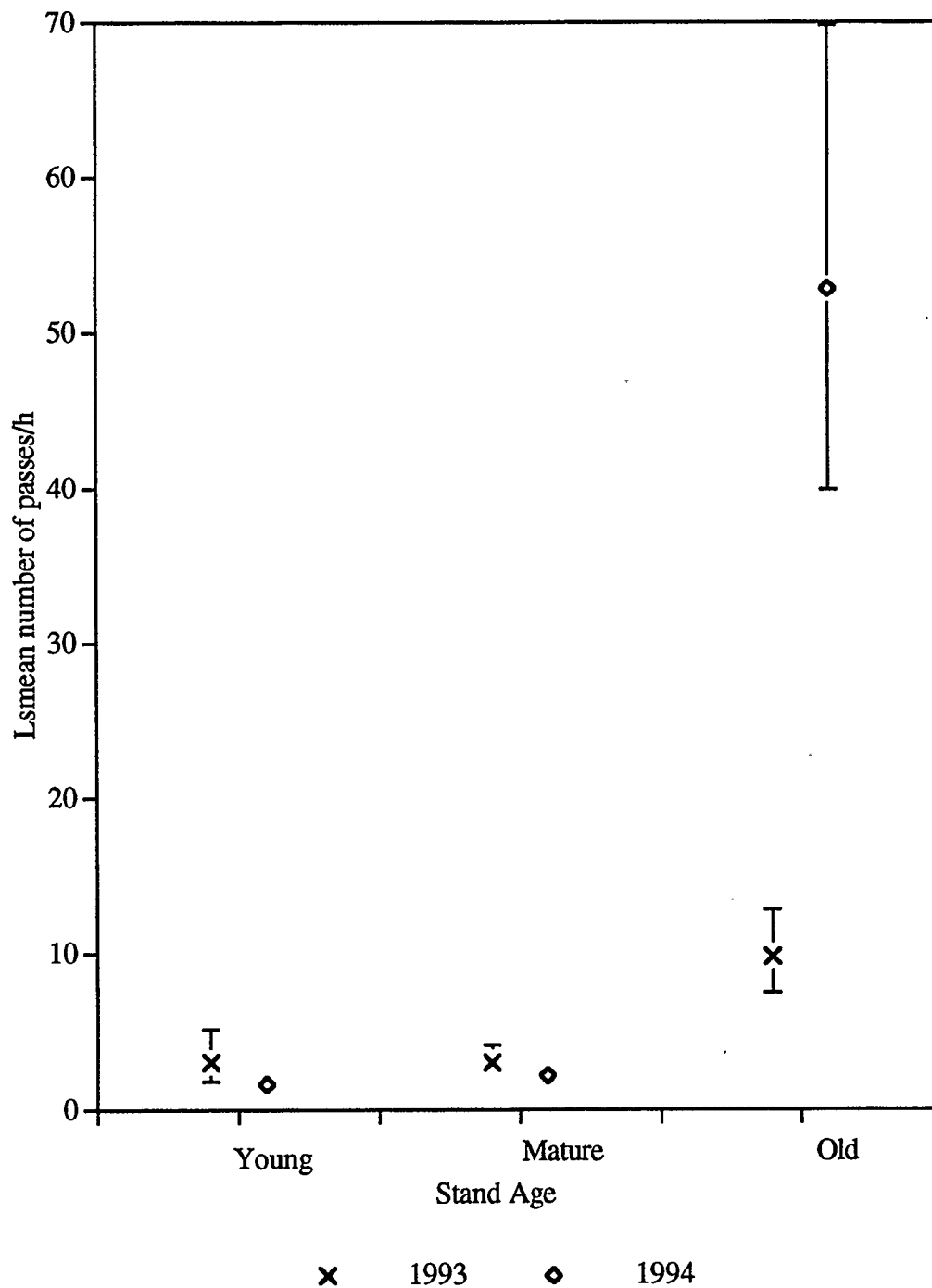
Figure 2.5. Least squares mean number (± S.E.) of total bat passes/h detected in aspen mixedwood stands of different ages in 1993 and 1994. Means are based only on sites in which at least one bat was detected, and calculated from log-transformed data, thus S.E.'s are asymmetrical. 1993 Young: n=7, Mature: n=16, Old: n=21; 1994 Young: n=10, Mature: n=7, Old: n=11.

During all-night sampling, there was no significant difference in total bat activity among periods of the night in any age. Young and mature stands had uniformly low activity (Figure 2.6). In young stands, maximum activity of 2.62 passes/2h occurred during the night, compared to minimum activity of 0.98 passes/2h in the evening (F =1.03; df=2,12; P > 0.3). In mature stands, activity ranged from 2.23 passes/2h in the evening to 2.90 passes/2h in the morning (F =0.35; df=2,14; P > 0.7). Minimum activity in old stands was 22.8 passes/2h in the morning and maximum activity was 38.7 passes/2h in the night period; the activity over all three periods did not differ significantly (F =0.55; df=2,18; P > 0.5), but was greater than peak activity of the other two ages.

In 1993, mean total bat (Figure 2.7; median activity plotted) and *Myotis* activity appeared to be higher in old stands 1 and 3 (O1 and O3) and mature stand 4 (M4), than in other old and mature stands, respectively. In 1994, mean total activity was again highest in O1. When all stand ages were considered together (ANOVAs of stand nested within age), there was no difference among stands. However, when each age was considered separately (in the two-way ANOVA of year and stand, which examined only unfragmented stands), old stands (O1 and O4) differed (F = 5.03; df=1,10; P < 0.05). There were no differences among stands in mature forests, but M4 was not included in this analysis as it had been logged. Mean total bat detections was uniformly low in young and mature stands (other than M4 in 1993) in both years.

In stands where high activity was recorded, I often detected elevated numbers of passes near large gaps (>20 m^2) within the sites. The high mean activity in M4 was primarily due to the activity recorded at a large gap in one site.

Relative foraging activity and foraging habitat

Foraging activity was generally low in most sites, although it was high in a few sites near large gaps. I heard a total of 127 buzzes in 129 hours (0.98 buzzes/h) in 1993, and 74 buzzes in 88 hours (0.84 buzzes/h) in 1994. When I compared only the sites that
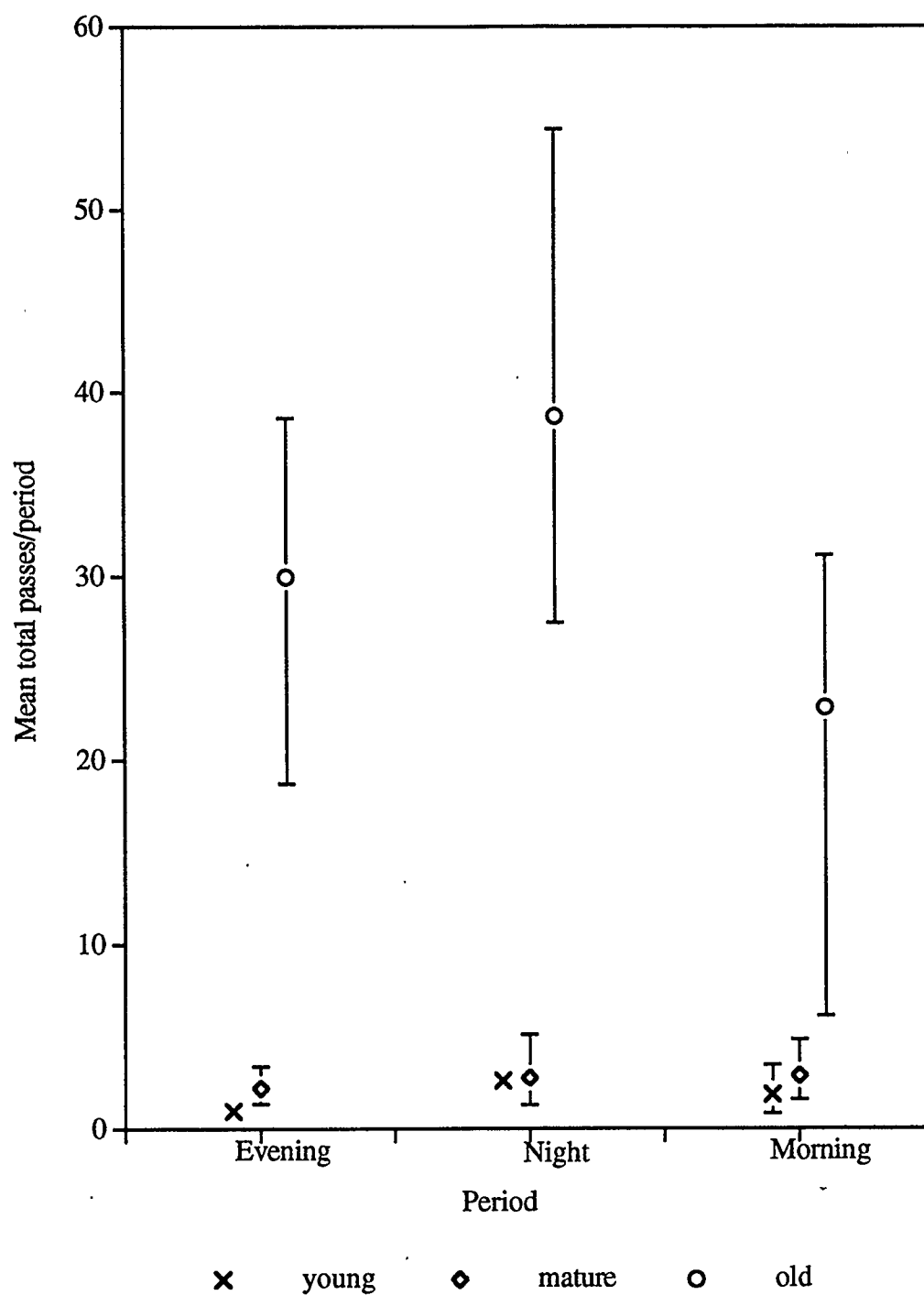
Figure 2.6. Mean (± S.E.) total number of passes in three periods of the night in different ages of aspen mixedwood forest. Means and S.E.'s were calculated from log-transformed data and thus S.E.'s are asymmetrical. n=7 young, 8 mature and 10 old sites.
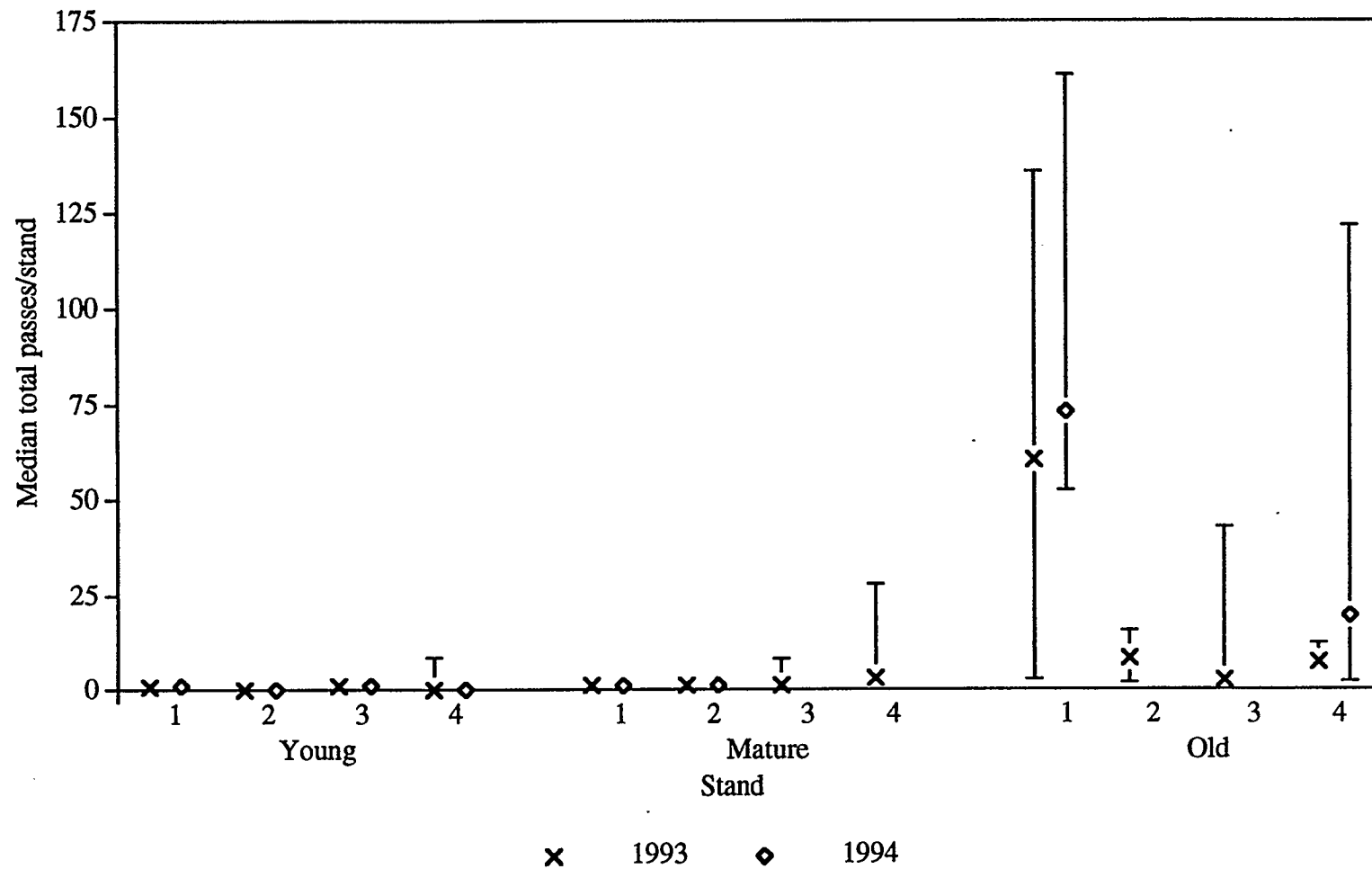
Figure 2.7. Median total number of passes (with 25% and 75% quartiles) detected in different aspen mixedwood stands, 1993 and 1994. Y1: n=4, Y2: n=5, Y3: n=5, Y4: n=5; M1: n=6, M2: n=5, M3: n=6, M4: n=6; O1: n=6 O2: n=6, O3: n=6, O4: n=5; M3, M4, O2 and O3 were logged in 1994 and values for that year are not included.

were sampled in both years, and equalised sampling effort in terms of number of hours/site, total and *Myotis* foraging activities were similar in the two years (Table 2.2). *L. noctivagans* foraging activity, however, was lower in 1994 than in 1993 (1993=35.0 buzzes; 1994=9.1). The same trends were observed when foraging rate (the ratio of buzzes to passes) was compared between the two years (Table 2.2).

Most feeding buzzes (70% in 1993; 90% in 1994) were emitted by *Myotis*. However, when *Myotis* and *L. noctivagans* foraging rates were compared for 1993, *Myotis* foraging effort (0.08 buzzes/pass) was lower than that of *L. noctivagans* (0.24 buzzes/pass). In 1994, *Myotis* had a greater foraging rate than did *L. noctivagans* (*Myotis* =0.09; *L. noctivagans* =0.04 buzzes/pass).

In both years, total foraging activity was greater than expected in old stands and lower than expected in young and mature stands combined (1993: χ^2=53.5; df=1; $P <$ 0.001; 1994: χ^2=167.0; df=1; $P < 0.001$; Figure 2.8). *Myotis* foraging activity was also significantly greater in old stands in both years (1993: χ^2=69.2; df=2; $P <0.001$; 1994: χ^2=147.8; df=2; $P < 0.001$; Figure 2.8). In 1994, I detected no *Myotis* foraging activity in young stands. In 1993, *L. noctivagans* foraged slightly more than expected in old and young stands combined, and less than expected in mature stands (χ^2=7.91; df=1; $P <$ 0.005) but in 1994 they foraged exclusively in old stands (χ^2=24.0; df=1; $P < 0.001$).

I also compared the ratio of the number of buzzes to the number of passes (foraging rate) among stand ages (Table 2.3), but was unable to perform statistical analyses due to limited data and high variation. Total foraging rates ranged from 0.05 to 0.31 buzzes/pass over the two years. In 1993, although few bats were detected in young stands, relative to the number of passes, the foraging activity was high compared to that of old or mature stands. *Myotis* and *L. noctivagans* foraging rates were also higher in young stands. These buzzes were all detected in one site, however. In 1994, foraging rates were low in

Table 2.2. Bat foraging activity and foraging rate in aspen mixedwood forests, 1993 and 1994. Both activity and effort were calculated over two hours [activity/2h = (# buzzes/# minutes of monitoring) x 120 minutes].

Species	Activity (# buzzes)		Rate (#buzzes/passes)	
	1993	1994	1993	1994
Total bats	80.7	71.9	0.11	0.07
Myotis spp.	44.7	63.8	0.08	0.09
L. noctivagans	35.0	·9.10	0.24	0.04
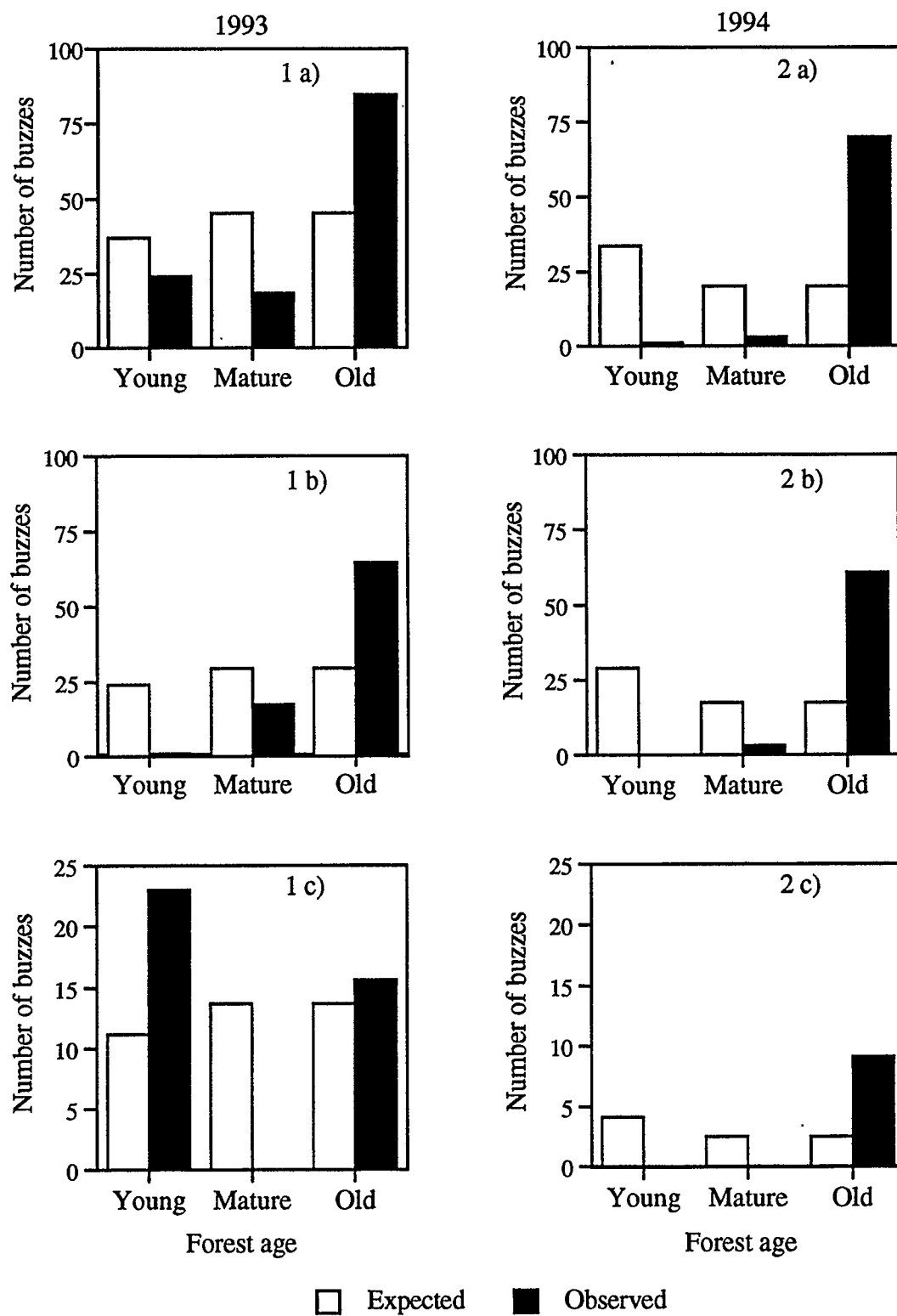
Figure 2.8. Comparison of observed to expected (based on sampling effort) number of feeding buzzes for different species groups in young, mature and old aspen mixedwood stands. In each year: a) total, b) *Myotis* spp., c) *L. noctivagans*.

Table 2.3. Foraging rates (# buzzes/# passes) of various bat groups in stands of different ages in the aspen mixedwood forest, 1993 and 1994. Rates were calculated over the two hours following sunset.

Stand Age	Foraging Rate (#buzzes/#passes)					
	Total Bats		*Myotis* spp.		*L. noctivagans*	
	1993	1994	1993	1994	1993	1994
Young	0.31	0.03	0.20	0	0.35	0
Mature	0.05	0.06	0.11	0.14	0	0
Old	0.09	0.07	0.08	0.08	0.17	0.04

all ages, and were lowest in young stands. No *Myotis* or *L. noctivagans* feeding buzzes were detected in young stands in 1994.

Radiotelemetry observations in 1994 indicated that in the first 60-90 minutes of the night, foraging bats stayed close to the roost tree, as they were rarely out of range (maximum detection range of the transmitters is < two km), and in fact often returned several times to the roost tree. Mean first emergence from trees was 24.0 ± 2.04 minutes after sunset; generally within 30 minutes of the first, all bats had emerged and the first bats were returning to the roost. Two nights of radiotracking at Touchwood Lake suggested that four radiotagged bats from a stand 2 km from the lake were not foraging over the lake, but rather in forested areas, possibly including smaller bodies of water within the forest.

Roosting behaviour

In 1994, I netted and radio-tagged bats in or near old stands 1, 2, and 4, mature stands 2 and 4, and young stand 4. I radio-tagged ten (one pregnant, four lactating, and five non-reproductive) female *M. lucifugus* from mature and old stands. Two of the non-reproductive females were never detected following release. The other eight bats were followed to 15 roost trees; some bats used two or even three trees. Two pregnant, one lactating, two post-lactating and one juvenile female *L. noctivagans* (n=6) were tracked to 11 roost trees. Additionally, one *M. lucifugus* was observed to emerge from a tree found during the site sampling program. Thus, a total of 27 trees were measured, all in old stands. Bats were observed emerging from 23 of these trees at dusk. However, based on radio signal characteristics, we were confident that we had correctly identified the other four roost trees. Moreover, the same conclusions were drawn from ANOVAs conducted with and without these four trees, so they were included in analyses of roost vs. random trees. In three trees, bats emerged from more than one roost entrance; a total of 28 roosts were used for analyses.

Myotis lucifugus and *L. noctivagans* used similar trees and roosts; in no case did the selection of tree characteristics differ between the two species (Table 2.4; $0.003 < F < 0.41$, $0.53 < P < 0.95$). All roost trees were *Populus* spp. *M. lucifugus* used 13 aspen (*P. tremuloides*), two balsam poplars (*P. balsamifera*), and one unidentified *Populus* spp. *L. noctivagans* used nine aspen, and two *Populus* spp. Roost trees were large; mean roost tree height was 22.3 m for *M. lucifugus* and 22.1 m for *L. noctivagans*. *M. lucifugus* and *L. noctivagans* used roost trees with tops on average 0.2 m and 1.1 m below the canopy, respectively. Mean roost tree DBH was 41.0 cm for *M. lucifugus* and 42.5 cm for *L. noctivagans*.

Myotis lucifugus and *L. noctivagans* both roosted predominantly (19/28 roosts) in deep cavities which appeared to have originated as cracks, scars or knot holes. Seven of these 19 roosts were in deep woodpecker feeding and nesting cavities. Although most of the roost trees were not of advanced decay, they may have had some heart rot that formed cavities in the trees (I could not see the back of most of the roosts). These roosts held the largest colonies (6-60 bats; 15 roosts), although two of them housed single bats. Two *M. lucifugus* roosts (of two and four bats) were under loose bark, both in trees of decay class D3/D4. *L. noctivagans* was not observed to use loose bark, but one female roosted singly in a shallow crack. In total, eleven roosts held fewer than five bats. Mean and median colony sizes were similar for *M. lucifugus* (15.3 and 7.5 bats respectively) and *L. noctivagans* (9.1 and 7.0 bats respectively; Table 2.4). Maximum colony size for *M. lucifugus* was 60 bats, and for *L. noctivagans* was 24 bats. Similar roost heights were used by the two species (11.4 m for *M. lucifugus* and 11.0 m for *L. noctivagans*), and did not appear to depend on roost type.

Colonies were transient (mean residency time: *M. lucifugus* $=3.67 \pm 0.56$, n=6; *L. noctivagans* $= 2.67 \pm 1.2$; n=3; both species $= 3.3 \pm 1.6$ days; Table 2.4). Bats did not remain together, as individuals from a colony moved to different trees. Bats often moved

Table 2.4. Characteristics of trees and roosts used by *M. lucifugus* and *L. noctivagans* in aspen mixedwood forests, 1994. For each characteristic, means and S.E.'s are shown. The F and P values refer to the nested ANOVA testing differences in species preferences. Also included are three measures of roosting behaviour: residency, colony size, and distance between consecutive roost trees.

Tree and Roost Characteristics	*Myotis lucifugus* n=16 trees	*Lasionycteris noctivagans* n=11 trees	F	P
Tree:				
DBH (cm)	41.0 ± 1.88	42.5 ± 3.46	0.41	0.53
Tree Height (m)	22.3 ± 1.70	22.1 ± 2.25	0.003	0.95
Distance to Canopy (m)	-0.2 ± 1.29	1.10 ± 0.98	0.41	0.53
Percent Bark	93.1 ± 2.62	95.5 ± 1.42	0.11	0.74
Canopy Depth (m)	3.84 ± 1.30	4.00 ± 2.00	0.03	0.86
Percent Leaf	26.9 ± 8.90	27.3 ± 12.1	0.06	0.82
% Bare Trunk	71.6 ± 4.44	65.5 ± 7.21	0.11	0.74
Tree Distance (m) †	1050 ± 251.7 (n=9)	280 ± 66.3 (n=5)	-	-
Roost:				
Roost Height (m)	11.4 ± 1.27 (n=17 roosts)	11.0 ± 1.36 (n=11 roosts)	0.03	0.86
Roost Width (cm)	7.37 ± 0.91 (n=16)	5.18 ± 1.05 (n=11)	-	-
Residency (days)	3.67 ± 0.56 (n=6)	2.67 ± 1.20 (n=3)	-	-
# Bats	15.3 ± 4.55 (n=16)	9.10 ± 2.27 (n=10)		0.83*

† Tree distance is the horizontal distance between consecutive roost trees
* Mann Whitney test
- not calculated

several hundred metres between roost trees, and sometimes moved more than a kilometre (n=4). Mean distance between successive roost trees was approximately 775 ± 710 m (n=14; Table 2.4). Roost trees used by the same bat were always connected to each other by forested areas (including stands of the same or other ages or species). Two bats roosted in trees in cutblocks, but neither tree was far (18 m and 25 m) from the forest edge, although other wildlife trees were found throughout the cutblocks.

Bats never returned to a roost tree after roosting elsewhere during the period in which I tracked them. In one case, I tracked a *L. noctivagans* to a tree, but was unable to observe it that night. The next night, *Myotis* spp. emerged from that tree. I considered it to be a *L. noctivagans* tree. Additionally, one roost tree had been used formerly by a northern flying squirrel (*Glaucomys sabrinus*; L. McDonald, pers. comm.).

I measured a total of 127 random wildlife trees in mature and in old stands, and 112 random trees in young stands. On two occasions in mature stands, and eight occasions in young stands, I was unable to find a tree fitting the wildlife tree criteria within the 25 m search radius. I was always able to find a random wildlife tree in old sites.

Two variables, tree height and percent leaf, significantly discriminated between roost and random trees in old stands. Tree height was the first variable entered in the stepwise discriminant functions analysis; it explained 11.9% of the variation between the two groups, whereas percent leaf accounted for 22.2% of the variation (Table 2.5).

The centroid for roost trees lay at the negative end of the canonical axis, and the centroid for random trees at the positive. The negative TCSC for tree height indicates that roost trees tend to be taller, and the positive TCSC for percent leaf indicates that they tend to be of lower percent leaf, than old-stand random trees. The classification error rates for random and roost trees were 29.6% and 29.9% respectively, for a total of 29.7%.

Tree height was significantly positively correlated with DBH, percent bark, and canopy depth and significantly negatively correlated with distance to canopy and percent

Table 2.5. Summary of stepwise discriminant functions analysis and canonical discriminant functions analysis comparing tree characteristics of roost trees and random wildlife trees found in old aspen mixedwood forests. The magnitude and sign of the Total Canonical Structure Coefficient (TCSC) for each variable gives its position on the discriminant axis. The centroids for roost and random trees are found at the negative and positive ends of the discriminant axis, respectively.

Variable	Order Included	Partial R^2	F Statistic	P value	TCSC
Tree Height	1	0.119	11.6	0.0010	-0.542
Percent Leaf	2	0.222	24.3	0.0001	0.503

bare trunk (Table 2.6). Percent leaf was significantly positively correlated with percent bark and canopy depth and significantly negatively correlated with DBH, distance to canopy and percent bare trunk. Most other significant correlations were negative, including percent bark and distance to canopy, percent bark and canopy depth, canopy depth and distance to canopy, and canopy depth and percent bare trunk. DBH and distance to canopy were both significantly positively correlated with percent bare trunk.

Roost trees were also taller, and had lower percent leaf than random trees in young and mature stands (Table 2.7; Figures 2.9 and 2.10); few trees in young or mature stands were of mean roost tree height. Furthermore, more roost trees had moderate leaf cover (20-70%) than did random trees, particularly in young and old stands; most random trees had leaf cover in the 0-9% range, or the 70-100% range. Random trees in these ages were also of lower DBH, were further below the canopy, and tended to be more cluttered.

Bats did not select roost trees at random with respect to species; they preferred *P. tremuloides* over other species present among old random trees (randomisation test: $G = 10.6$, $P < 0.025$; Figure 2.11). The relative proportion of aspen trees used as roosts, and aspen random trees in mature stands was similar. In young stands, more random trees were of unidentified *Populus* spp., or other species. Roost trees were more likely to have rot than were old-stand random trees (Yates' $\chi^2=4.61$; df=1; $P < 0.05$). Few trees in mature, but many trees in young stands showed evidence of rot (Figure 2.12). However, bats preferred trees of decay classes D1 and D2, given their low abundance among old random trees (randomisation test: $G =12.6$, $P < 0.025$), and these trees were not abundant among young- and mature-stand wildlife trees (Figure 2.13). The preference for trees of moderate canopy class ($\chi^2=6.40$; df=2; $P < 0.05$), which are unusual amongst wildlife trees in all ages (Figure 2.14), may reflect the selection of these decay classes. All other characteristics (e.g. top condition, distance to edge) were used according to their availability among old random trees.

Table 2.6. Correlation matrix of roost- and old-stand random tree variables included in discriminant functions analysis.

Variable	Height	% Leaf	DBH	Distance to Canopy	% Bark	Canopy Depth
% Leaf	0.45***					
DBH	0.23*	-0.32**				
Distance to Canopy	-0.79***	-0.39***	-0.16			
% Bark	0.33***	0.33**	0.02	-0.24*		
Canopy Depth	0.58***	0.85***	-0.10	-0.40***	-0.52***	
% Bare Trunk	-0.34***	-0.58***	0.41***	0.29**	-0.11	-0.51***

* $P < 0.05$
** $P < 0.01$
*** $P < 0.001$

Table 2.7. Comparison of mean and standard error of several characteristics (continuous variables from DFA) of trees used as roosts, to those of random trees in old, mature and young stands. The old random tree sample includes only the first tree of each pair sampled at each bearing in each site, whereas samples from the other ages include both trees of each pair.

Tree Characteristic	Roost Trees (n=27)	Old Random Trees (n=64)	Mature Random Trees (n=127)	Young Random Trees (n=112)
Tree Height (m)	22.2 ± 1.33	17.1 ± 0.99	15.2 ± 0.48	8.35 ± 0.50
% Leaf Remaining	27.0 ± 7.06	52.5 ± 5.16	56.1 ± 3.54†	43.9 ± 4.19
DBH (cm)	41.6 ± 1.76	31.3 ± 1.66	16.9 ± 0.72†	17.4 ± 0.785
Distance to Canopy (m)	0.32 ± 0.86*	5.48 ± 0.95	3.17 ± 0.48	2.84 ± 0.43
% Bark Remaining	94.1 ± 1.65	91.4 ± 2.10	94.1 ± 1.13††	65.8 ± 3.74¥
Canopy Depth (m)	3.91 ± 1.10	6.07 ± 0.71**	4.21 ± 0.28†	2.60 ± 0.26
% Bare Trunk	69.1 ± 3.90	49.9 ± 4.44	43.6 ± 2.63	52.9 ± 4.16

* n=25
** n=63
† n=126
†† n=124
¥ n=108
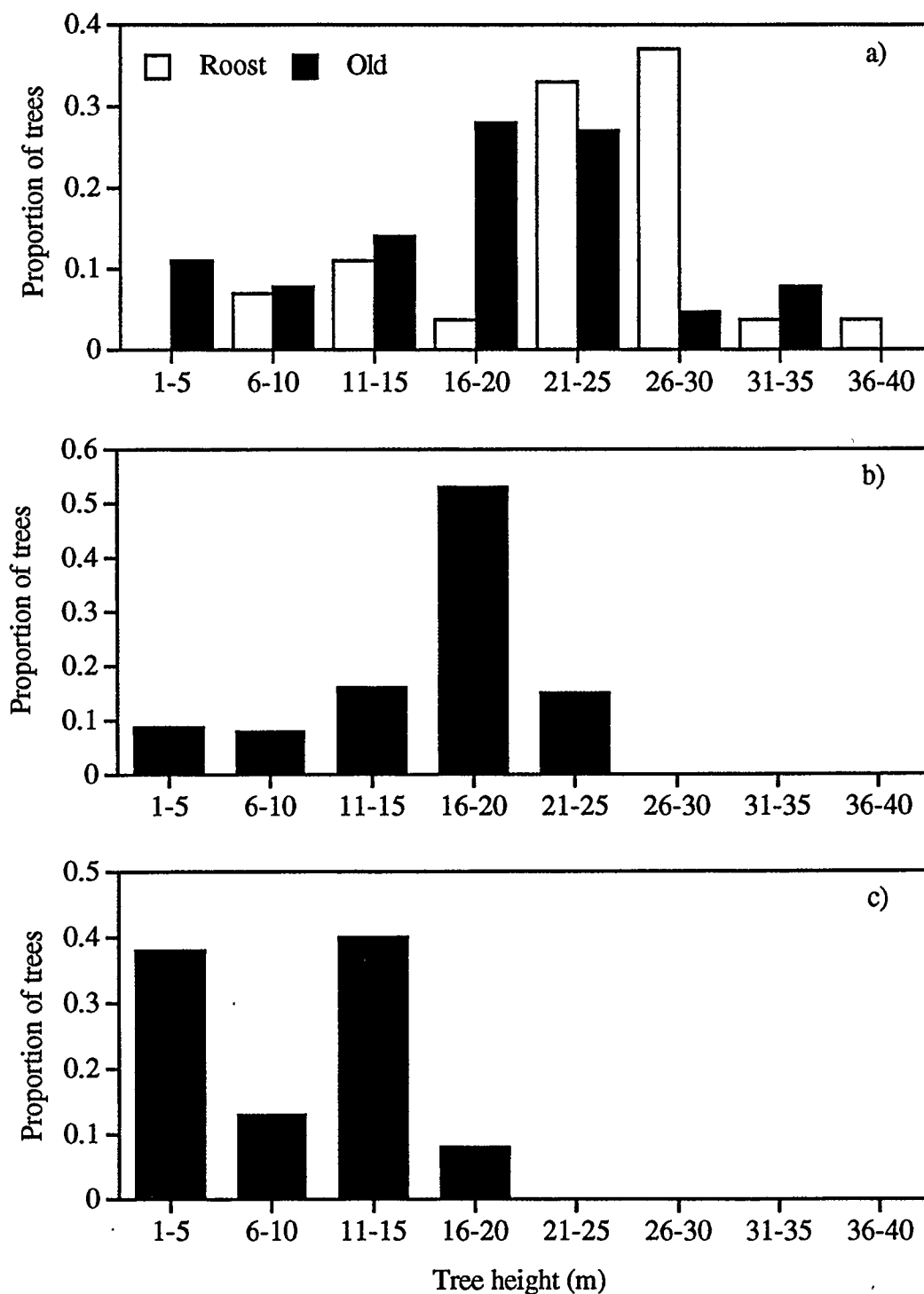
Figure 2.9. Relative proportions of trees of different heights in samples of a) roost trees, and random trees in old, b) mature, and c) young aspen mixedwood stands. Roost: n=27, Old: n=64, Mature: n=127,Young: n=112. For old sites, I included only the first random tree at each bearing; for young and mature sites, I included both trees.
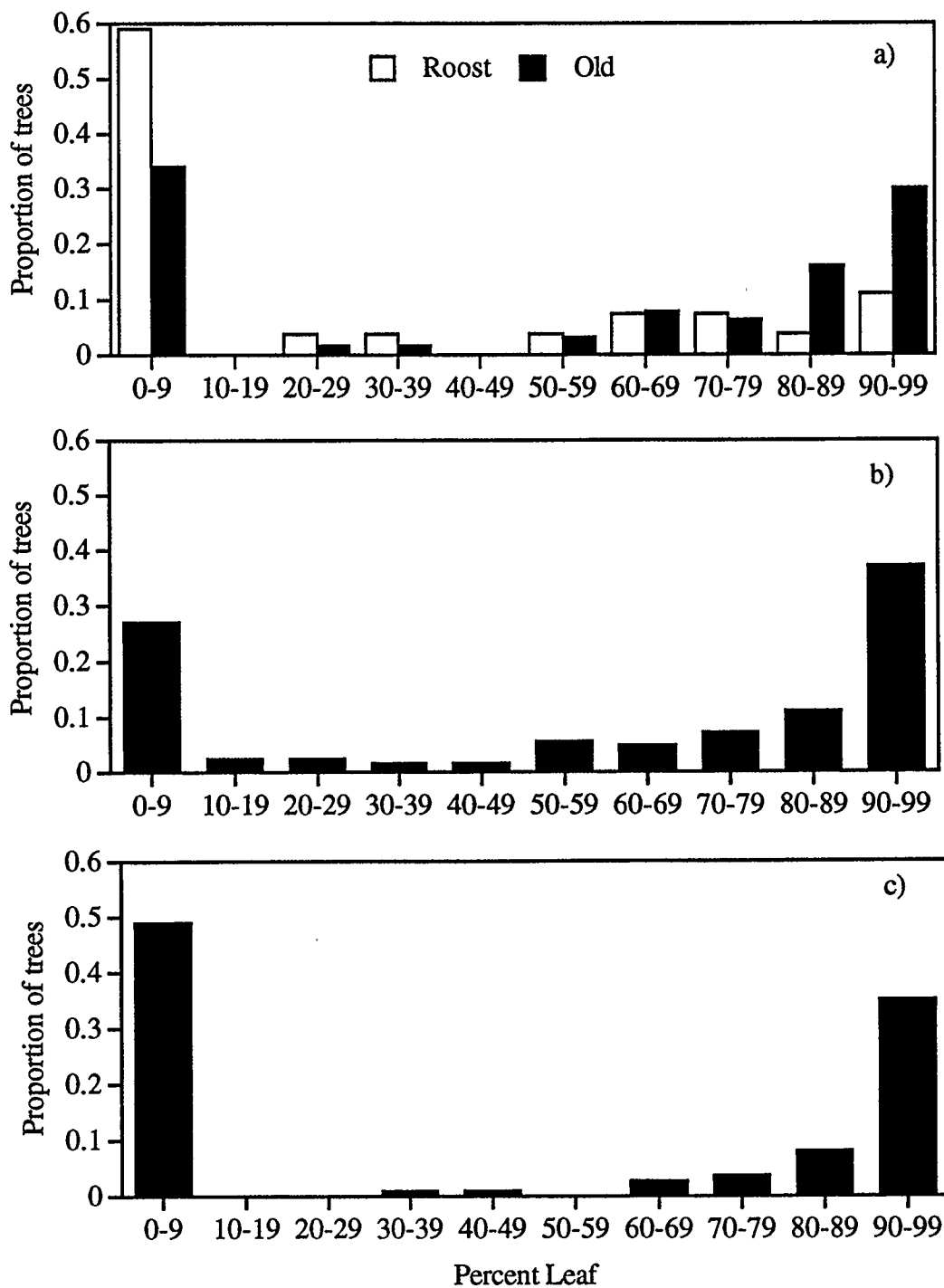
Figure 2.10. Relative proportions of trees with different amounts of remaining leaf in samples of roost trees, and random trees in a) old, b) mature and c) young aspen mixedwood stands. Roost: n=27, Old: n=64, Mature: n=127, Young: n=112. For old sites, I included only the first random tree at each bearing, and for young and mature sites, I included both trees.
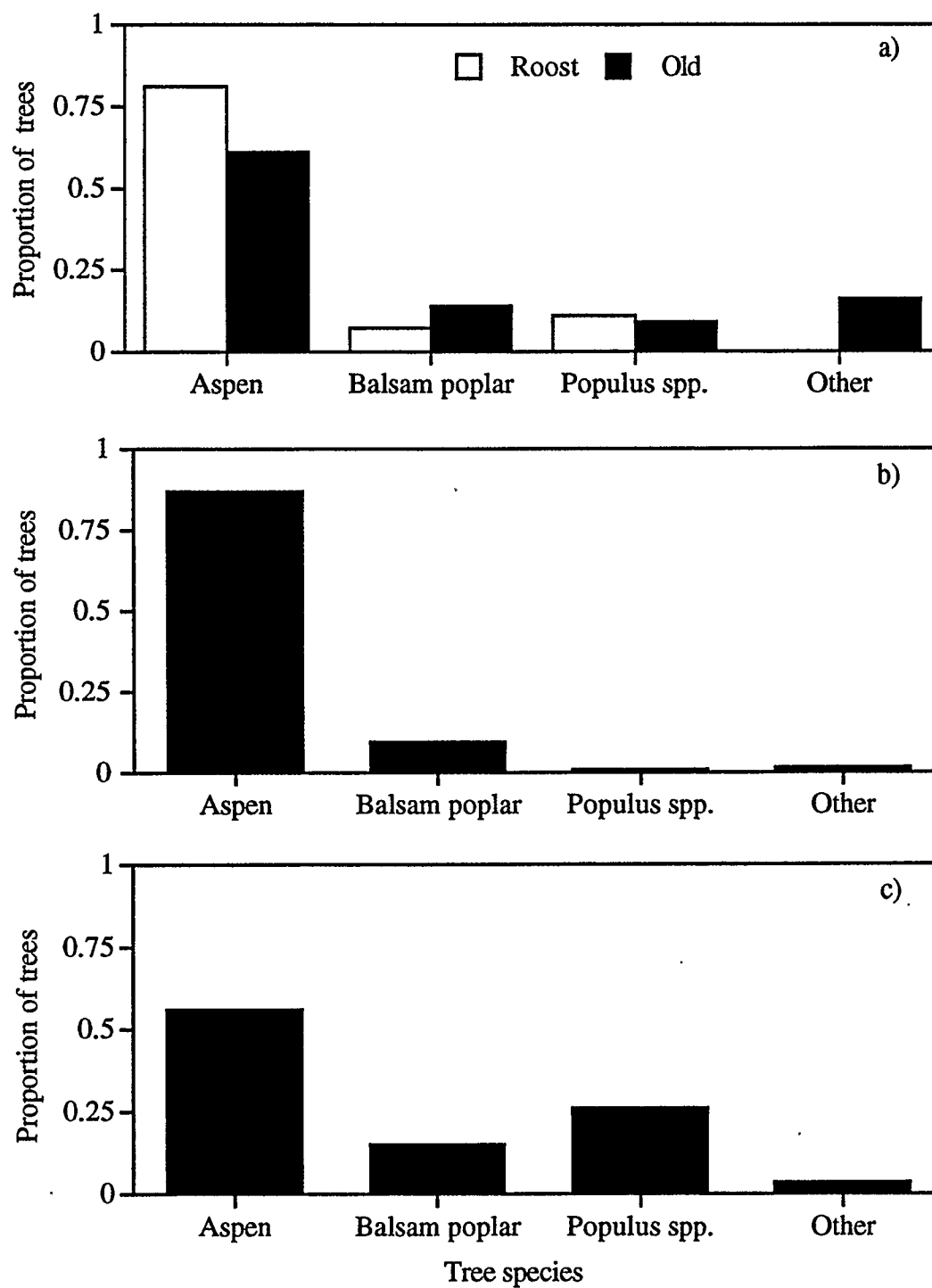
Figure 2.11 Relative proportions of trees of different species in samples of of a) roost trees and random trees from old, b) mature, and c) young stands. "Other" includes birch, willow and spruce. Roost: n=27, Old: n=127, Mature: n=127, Young: n=110. In all ages, I included both trees at each bearing in each site.
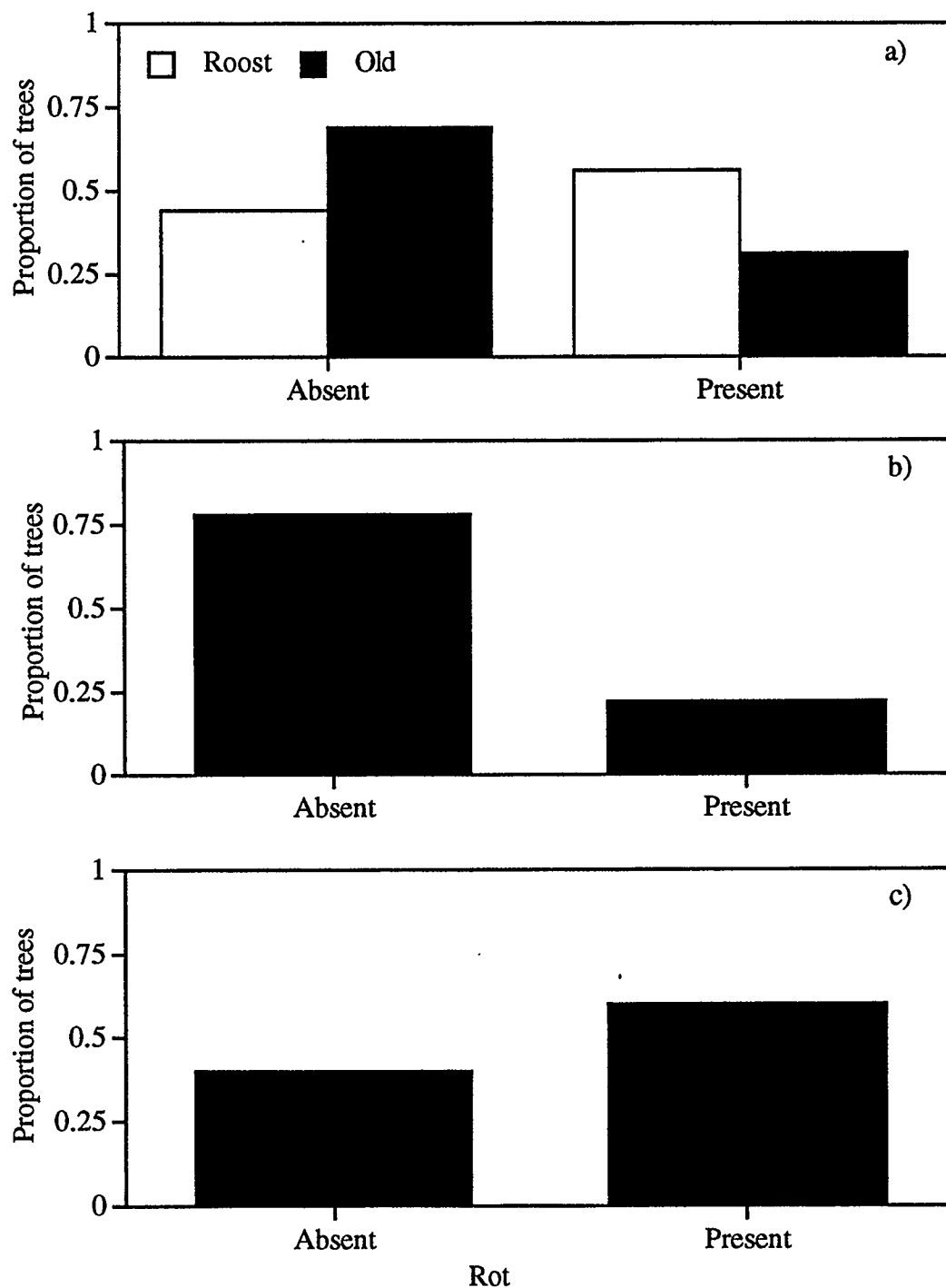
Figure 2.12. Relative proportions of trees with and without rot in samples of
a) roost trees, and random trees from old, b) mature and c) young aspen
mixedwood stands. Roost: n=27, Old: n=127, Mature: n=127, Young:
n=109. In all ages, I included both trees sampled at each bearing in each site.
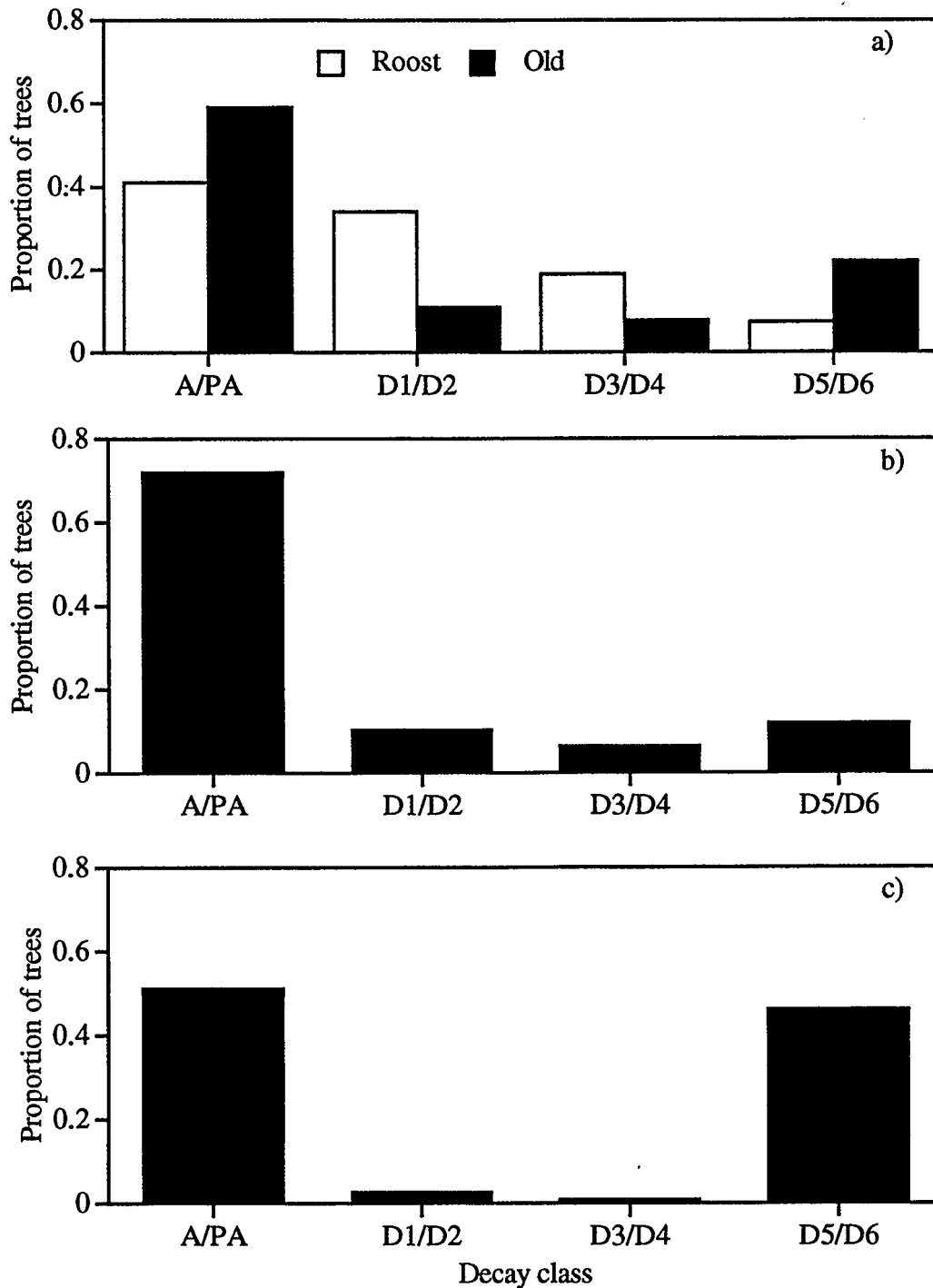
Figure 2.13. Relative proportions of trees in different decay classes in samples of a) roost trees, and random trees from old, b) mature, and c) young aspen mixedwood stands. Roost: n=27, Old: n=127, Mature: n=127, Young: n=112. In all ages, I included both trees sampled at each bearing in each site.
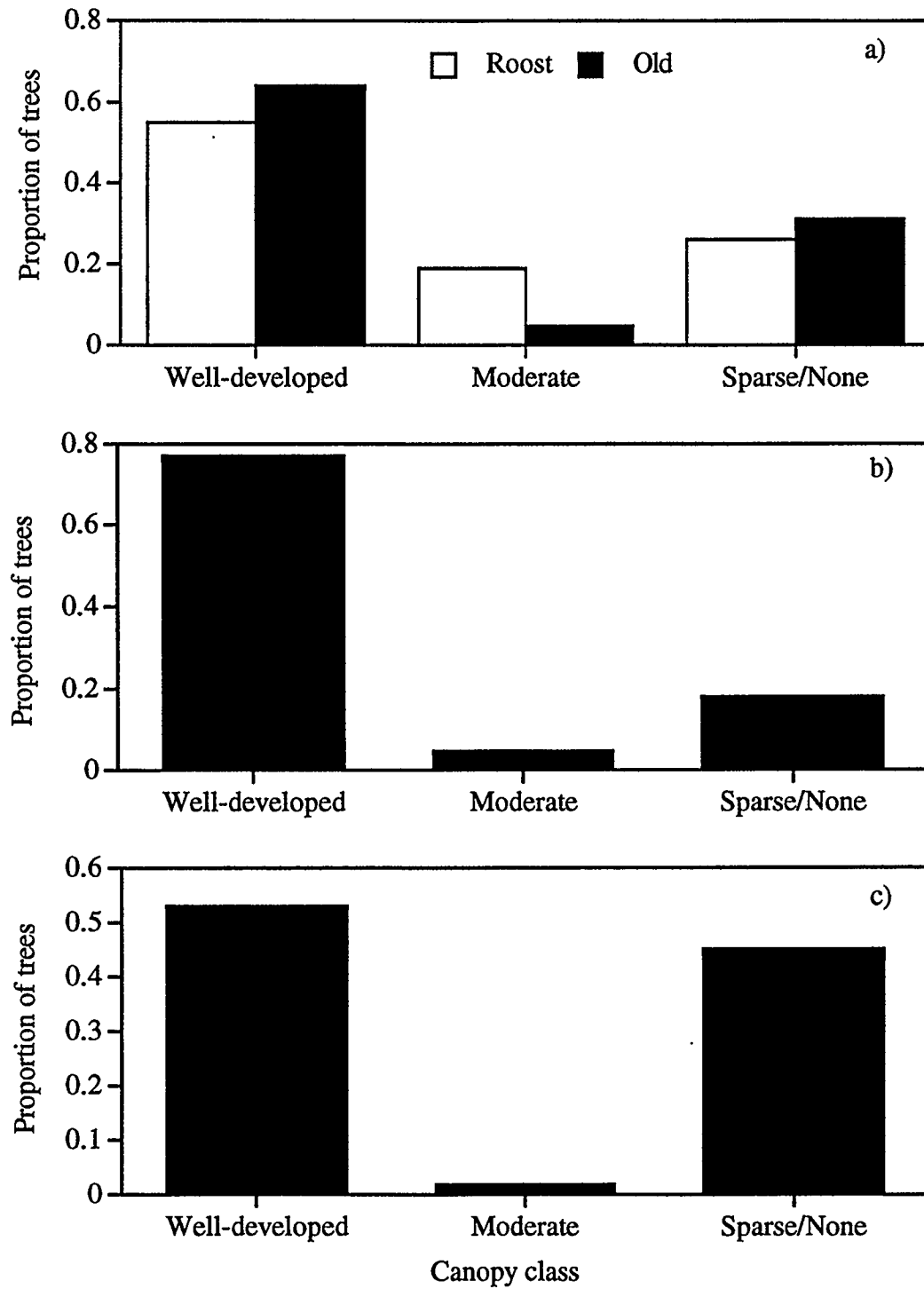
Figure 2.14. Relative proportions of trees with different canopy classes in samples of a) roost trees, and random trees from old, b) mature and c) young aspen mixedwood stands. Roost: n=27, Old: n=127, Mature: n=127, Young: n=112. In all ages, I included both trees measured at each bearing in each site.

Bats showed a strong preference for deep cavity roosts, given their low abundance in old-stand wildlife trees, (randomisation test: $G = 126.5$, $P < 0.001$). These roosts are also scarce in young and mature stands (Figure 2.15). Given their relative abundance, bats avoided using loose bark and shallow cavities as roosts. Roosts may have been selected for their height, as much loose bark present on old wildlife trees occurs low down on the trunk. On old-stand random trees, I measured 56 loose bark pieces that were large enough to hold several bats, and 71 pieces that could hold one or two bats (Barclay et al. 1988); only six pieces of 71 (8.4%) were 11 m (mean roost height) or higher. Forty five (63.4%) of these 71 pieces were higher than 2 m (the minimum roost height recorded, which was for a crack). Mean height for loose bark roosts was 11.3 m, and minimum was 8.0 m. Roosts may also have been selected for their depth, as many moderately deep (10-30 cm) cavities in random trees were higher than the mean roost height (3/5 woodpecker feeding cavities) but these cavities were not used during my study.

Discussion

The distribution of bats in the aspen mixedwood forest reflects species-specific roosting and foraging habitat preferences. The five species of bats identified in the forest were not equally abundant. The bat community was dominated by *Myotis* spp. (probably *M. lucifugus*, given this species' high rate of capture) and *L. noctivagans* and breeding populations of both these species occurred in the boreal forest. *M. lucifugus* and *L. noctivagans* are adapted to deal with cluttered environments (Barclay 1991, Saunders and Barclay 1992) such as forests. *L. cinereus* may also breed in the area, but is uncommon, as is *E. fuscus*, perhaps because the fast flight and long range prey detection of these two species (Barclay 1985, Norberg and Rayner 1987, Fenton 1990, Barclay and Brigham 1991) makes them less suited for this forest. Alternatively, they may occur in lower numbers than *M. lucifugus* and *L. noctivagans* at this latitude, even in other habitats. Because of the low abundance of *L. cinereus* and *E. fuscus*, I will not discuss their
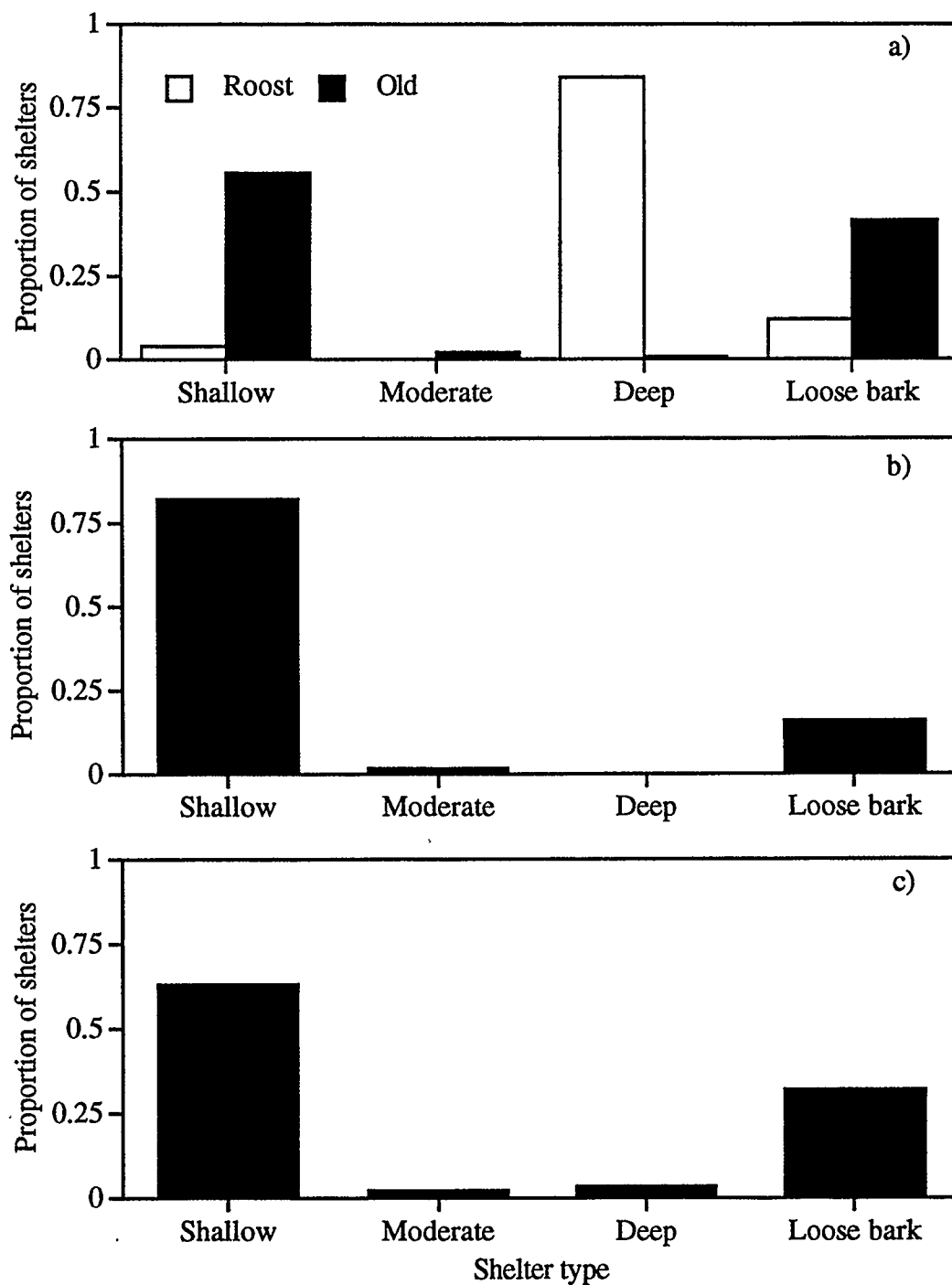
Figure 2.15. Relative proportions of different types of shelter (based on depth and type) found in a) roost trees, and random trees in old, b) mature and c) young stands. Cavities and cracks: shallow (1-10 cm deep), moderate (11-20 cm deep), deep (> 20 cm). Loose Bark: 2-50 cm deep. Roost: n=25, Old: n=284, Mature: n=219, Young: n=179 shelters.

preferences for habitats within the aspen mixedwood, although they are included when I discuss total bat abundances.

Relationships between bat abundance and stand age

Within the aspen mixedwood forest, bats were not evenly distributed among stand ages. Bat abundance, based on captures in both the site sampling and radio programs, was greatest in old stands. Bats did not appear to consistently avoid or prefer the other two ages; in site sampling, they avoided young stands, but in the radio tracking program, they avoided mature stands. In coniferous systems, captures were also higher in old forests (100 + years) than in other ages (Perkins and Cross 1988). Within Douglas-fir forests, but not Ponderosa pine, more bats were captured in mature than in young stands (Perkins and Cross 1988).

Bat occurrence in both years, and activity in 1994, based on echolocation call detection, were also highest in old stands. In 1994, occurrence was higher in old stands than in both the other ages, but in 1993, it was greater in old stands than in young, but not mature stands. Lower 1993 temperatures may have depressed bat abundance and activity, by reducing reproductive success (Fenton et al. 1980, Grindal et al. 1992, Lewis 1993), and the number of bats in flight (Grinevitch et al. 1995, Wilkinson 1995) and duration of flight (Anthony et al. 1981, Barclay 1985, Rydell 1989a, Maier 1992). Lower activity and abundance in the aspen mixedwood forest reduced sample size in 1993, and made it more difficult to detect differences in abundance among stand ages

Bat occurrence may involve a single pass, or transient activity, by a bat. However, high activity results from a greater number of bats, and/or a greater amount of time spent foraging and commuting in the area by each bat. Thus increased activity in old stands in 1994 suggests that these stands are preferred by bats over the other ages. In the Pacific Northwest, occurrence and activity of a number of bat species were also greater in old Douglas-fir stands than in young and mature forests, which did not differ (Thomas 1988).

In some cases, as in the aspen mixedwood in 1994, bats appear to perceive the forest as being of two ages: "old" and "younger" (Thomas 1988), and do not use intermediate age classes differently from younger age classes. Old forests may contain habitat features required by bats that are not present in any other ages.

Some species of bats may be more prone than others to perceive a sharp distinction between old and younger forests. *Myotis* spp. made a stronger distinction between old aspen mixedwood and other ages (paralleling findings in coniferous forests of the Pacific Northwest: Thomas 1988) than the bat community in general. Although 1993 occurrence of total bats in old stands did not differ from that in mature stands, in both years *Myotis* occurrence in old stands was greater than that in mature stands. *L. noctivagans*, on the other hand, showed no clear preference for any age of aspen mixedwood forest in either year. In coniferous forests, however, the abundance of *L. noctivagans* was greater in old stands than in younger stands (Perkins and Cross 1988, Thomas 1988). In terms of ecomorphology (Norberg and Rayner 1987) and roosting behaviours (see below), *L. noctivagans* and *M. lucifugus* are similar, and I cannot account for the lack of a clear habitat preference in the former.

The echolocation call, wing design, dietary preferences, and roosting requirements of this bat community, and of some species in particular, may lead to this preference for old stands. The lack of habitat preference among other species may reflect differences in their requirements. Foraging opportunities may be greater in old aspen mixedwood forests due to reduced clutter (Lee et al. 1995a), or perhaps greater insect densities. Old stands have lower densities of trees; they also have more gaps (Lee et al. 1995a) and thus more edges, which are often used by many species of bats (Barclay 1985, 1991; Rydell 1986, 1989b; Furlonger et al. 1987, see also Chapter 3). Old stands have greater densities of large wildlife trees (see below and Lee et al. 1995a and b) and thus also offer better roosting opportunities than young and mature stands.

Relative Foraging Activity and Foraging Habitat

There were several indications that increased bat abundance in old aspen mixedwood stands may in part result from better foraging opportunities. Differences among foraging rates were slight, but rates were highest in young stands in 1993 (resulting from a series of attacks in a single site), and in old stands in 1994. Foraging rate (the number of buzzes to passes) represents the number of attacks made on insects relative to general commuting and foraging activity. Bats are often referred to as opportunists (Fenton 1982) and likely attack insects wherever they are, creating a reasonably consistent foraging rate. However, the higher numbers of passes and buzzes, and rate in 1994, indicate that bats are more attracted to old stands for foraging.

Similarly, *Myotis* spp. generally foraged more in old forests than in the other ages. Thomas (1988) also reported evidence that *Myotis* spp. forage at higher rates in old coniferous forests than in younger forests. Although many *Myotis* spp. have echolocation calls and wing designs that permit them to forage in clutter (Fenton 1990, Barclay 1991, Saunders and Barclay 1992), many, including *M. lucifugus*, prefer to forage in more open areas (Barclay 1991, Saunders and Barclay 1992), particularly if prey abundance is greater there (Brigham et al. 1992). In particular, *M. lucifugus* has been observed foraging along the edge of vegetation (Furlonger et al. 1987, Kalcounis and Brigham 1995), and thus may use the gaps present in old stands.

Over the two years, *L. noctivagans* did not show a strong tendency to forage in a particular stand age, reflecting their distribution among ages. This species is relatively slow and maneuverable (Norberg and Rayner 1987), and has been observed foraging in small gaps and using swarms of insects (Barclay 1985). Thus, it may be that *L. noctivagans* forages in small clearings in the forest in general, depending on local distributions of insects, and is not dependent on the larger gaps of old forests.

Availability of foraging opportunities may not be the driving factor in the selection of certain ages of aspen mixedwood forest by bats, given the abundance of lakes in the region. Bats (Rydell 1986, de Jong and Ahlen 1991), especially *M. lucifugus* (Barclay 1991, Saunders and Barclay 1992) and other *Myotis* spp. (Furlonger et al. 1987), often prefer water bodies to other habitats and will travel to them from roosts several kilometers distant (Brigham 1991, de Jong 1994). Increased prey availability may make the edges of deciduous forests along lake shores particularly good foraging habitat (de Jong 1994). Foraging rates over water bodies in the Pacific Northwest were approximately ten times greater than those within coniferous forest stands (Thomas 1988). Given the relatively low foraging rates in forests, Thomas (1988) concluded that they were not primary foraging sites, and that bats selected old forests for their better roost sites. Compared to the results of Thomas' (1988) study, foraging rates in the aspen mixedwood forest were generally intermediate between foraging rates over water bodies and foraging rates in the forest in the Pacific Northwest.

My results might suggest that bats were leaving the aspen mixedwood forest to forage over lakes, and that the forest primarily offered roosting locations. However, for several reasons, I conclude that bats may not be leaving the forest. First, there is no energetic basis for the concept of "low" foraging rate; the rate at which bats must forage to satisfy energetic demands is not known, and may depend on insect densities (Racey and Swift 1985). The rates observed in the aspen mixedwood forest may be sufficient, given other advantages to the bat, such as proximity to roost sites (given that flight is costly: Thomas 1987), and shelter from predators. Second, some studies have documented a preference by bats for forest interior and edge over other habitats, including water, perhaps reflecting increased prey density (Kalcounis and Brigham 1995) and shelter (de Jong 1994) in the first two habitats. Insect availability may also be high near roost trees, and may attract pregnant and lactating females (de Jong 1994). In my study, radiotagged *M.*

lucifugus and *L. noctivagans* remained close to, and often returned to, the roost tree, at least for the first part of the night. It is unlikely that they were at lakes, as the nearest ones were usually out of transmitter range during this period. Additionally, on the two nights we attempted to locate bats at one of the nearest lakes, they were detected foraging in the research stands beside the lake. On the other hand, these observations do not prove that bats were actually foraging within forested areas of the stands; bats may be foraging primarily over bogs, puddles and small clearings resulting from oil exploration within the forest. At this point, the importance of the aspen mixedwood forest in general, and old stands in particular, as foraging habitat cannot be clearly determined. I cannot completely elucidate the role of foraging behaviour in producing the observed high abundance of bats in old stands. Roost site selection may be more important.

Roosting behaviour and associations of roost trees with forest ages

In the aspen mixedwood forest, I found bat roost trees only in old stands. Comparison of tree and cavity characteristics between roost and random trees in old stands showed that female bats selected deep cavities in tall aspen trees that were of low percent leaf, early decay class, and moderate canopy class, and with rot. In young and mature stands, few wildlife trees matched these criteria, even in part. In particular, in young and mature stands, most wildlife trees were short and small, and of inappropriate decay class. Some trees in young stands were rotten, but these were generally pre-fire relic stumps (pers. obs.). Thus potential roost trees were scarce in these ages. Random trees in old stands best matched roost trees in terms of height, DBH and decay class. Increased roosting opportunities in old stands likely explain the high bat activity in these stands.

I focussed on roosts used by female bats because selection of an appropriate maternity roost environment is critical to bats' survival and reproductive success. Male bats may have less stringent requirements (Hamilton and Barclay 1994). For females, a warm roost makes it easier to maintain the high body temperatures (McNab 1982) required

for rapid fetal development (Racey 1973, Racey and Swift 1981). Given shorter summers at northern latitudes, it is especially important that parturition not be delayed so that young have time to grow and learn to forage before winter (Thomas et al. 1990). Colonial bats can maintain higher body temperatures than solitary animals (Trune and Slobodchikoff 1976, Roverud and Chappel 1991), so size of roost is also a factor. Furthermore, colonial animals may benefit from information sharing and may follow one another to profitable foraging areas (Wilkinson 1992). Individual bats emerging from colonies in groups may dilute their risk of being preyed upon (Hamilton 1991, Fenton et al. 1994). Roosts also must offer protection from predators such as mustelids, and larger potential competitors, such as *Glaucomys sabrinus*, which may use similar trees (L. McDonald, pers. comm.). The roost's height, depth, and entrance dimensions may deter predators and competitors. The characteristics of trees and roosts selected by bats in the aspen mixedwood reflect these factors: roosts in tall, large trees with rotten centres which can be accessed through deep cavities are likely warm, spacious, and protected from predators.

Tall trees and high roosts may receive more incident sunlight, causing them to be warmer (Humphrey et al. 1977, Kurta et al. 1993). Additionally, they tend to be close to the canopy and may be easier to locate and access. In some coniferous forests, bats also select tall trees (Vonhof 1995).

Tall trees also tend to be of greater diameter; roost trees were of much greater DBH than were random trees in any age. Cavities in large diameter trees can accommodate more bats. Roosts in these trees may also have thicker walls, and thus extra insulation, than those of small DBH, resulting in more stable roost temperatures (Sluter et al. 1973). Big trees remain standing for longer periods (Newton 1994), providing more enduring roost sites. Finally, some primary excavators prefer large DBH trees (Thomas 1979, Harestad and Keisker 1989), and may create appropriate bat roosts in these trees. In other forests, bats (e.g. Barclay et al. 1988, Lunney et al. 1988, Taylor and Savva 1988) and other

animals also prefer trees of large DBH (e.g. birds: Mannan et al. 1980, Rosenberg et al. 1988, Ohmann et al. 1994; squirrels: Maser 1981).

Trees of early decay class (= recently dead: D1 and D2) offer an optimum combination of important characteristics. Recently dead aspen are more likely than decayed trees to retain their tops and remain canopy trees. These trees generally have firm wood, which lessens their chance of blowdown, and improves insulation (Desch and Dinwoodie 1981), as does live wood (Humphrey et al. 1977). Yet these trees are not immune to events which cause heart rot and cavities inside the trees (Peterson and Peterson 1992). In fact, some primary excavators prefer trees of these decay classes (Erskine and McLaren 1971, Mannan et al. 1980, Harestad and Keisker 1989). Live and newly dead trees also retain most of their bark, which helps maintain suitable temperatures, and provides grip when animals land (Bendel and Gates 1987).

Low to moderate leaf cover may be associated with these decay classes. Alternatively, bats may actively select live and recently dead trees for this amount of cover, perhaps reflecting a tradeoff between decreased clutter from leaves (which might interfere with echolocation and flight, and thus access to the roost) and increased risk of predation (Jones et al. in press). Roost entrances were often situated in a dead, leafless branch (partly alive trees). The moderate canopy classes of D1 and D2 trees may again demonstrate that these classes provide an optimum combination of roost features.

Deep cavities high in trees also provide thermal and social benefits and may offer protection from predators. They are larger and probably more protected and warmer than the other types of shelters in wildlife trees. Loose bark pieces, while large enough to hold several bats, could not hold the numbers found in some of the cavities. Also, because aspen bark is generally thin, cavity roosts may have more stable and/or warmer temperatures, and are more humid (McComb and Noble 1981) than loose bark roosts. In

contrast, bats preferentially roost under loose bark in coniferous trees, where loose bark flaps are thicker and larger (Vonhof 1995).

By roosting relatively high in trees, bats may avoid clutter (Tidemann and Flavel 1987), as in old stands these roosts are in the less cluttered space above the subcanopy, but below the canopy. They may also experience less predation from ground-based predators. Bird nests placed lower in trees experience higher rates of predation and lower reproductive success than do those located higher (Rendell and Robertson 1989). There may be an upper limit to roost height imposed by DBH and the preferences of primary excavators (Harestad and Keisker 1989).

In the aspen mixedwood, bats switched roost trees often, despite the potential costs in terms of social interactions and familiarity with an area (Lewis 1995). Bats may switch roosts to avoid predation (Barclay et al. 1982, Fenton et al. 1994), to lessen parasite load (Marshall 1982, Fenton et al. 1993, Lewis 1993), or to take advantage of different microclimates (Lewis 1995). The persistence of healthy bat populations may depend on the availability of roosts for frequent switching. Suitable trees may be at such low density in young and mature stands that bats are unable to find sufficient alternate roosts.

If presence of cavities, and tree height, size and decay class are the most important features selected by bats, then the more abundant roosting opportunities of old stands may explain why I found roost trees in old stands only. Furthermore, there are several indicators that roost trees are limited even in old stands. First, as noted, even in old stands, some of the features selected by bats are not common (e.g. tall trees). Second, the decay classes selected by bats are short lived in aspen systems: D1 lasts a maximum of 10 years, and D2, an additional 10 (P. Lee, pers. comm.). Third, bats travelled long distances between alternate roosts. In other systems (Fenton 1983, Kurta et al. 1993, Vonhof 1995), bats move short distances, indicating that when possible, bats will move to nearby trees. In the aspen mixedwood forest, the events that create roost trees, such as disease,

may occur on a different scale or in different patterns than in these other woodlands, causing roost trees to be farther apart. Given their apparent scarcity, roost trees may drive habitat selection in aspen mixedwood forests, resulting in the observed patterns of bat abundance among forest ages.

The distribution of roost trees may explain some spatial and temporal patterns of bat activity in the forest. For example, old stands differ among stands in snag abundance (Lee et al. 1995b), and I have some evidence that they differ also in bat activity. Perhaps high activity is due to greater numbers of roost trees in those stands. The presence of roost trees may also explain timing of activity. The peak activity in hour 1 in old stands may reflect synchronised emergence of bats from roost trees (Kunz 1974, Swift 1980). Lower activity in hour 2 may indicate that bats have dispersed away from the roosts into other areas of the forest. High activity in the "night" period may reflect a second emergence, particularly of lactating bats (Swift 1980, Rydell 1993), or the steady return of bats (Maier 1992) to roost sites from foraging habitats. A nightly activity peak has been documented for some species (Leonard and Fenton 1983), including *L. noctivagans* (Barclay 1985). The absence of a predawn peak, typical in many regions and species (e.g. Kunz 1974, Swift 1980) could reflect either the shortness of northern nights, which makes one foraging period more profitable, and/or the generally low morning temperatures, which decrease insect abundance (Rydell 1989a) and often curtail bat activity (Rydell 1989a, Wilkinson 1995).

In summary, old stands support greater numbers of bats, particularly *Myotis* spp.. This abundance is associated with greater availability of roost trees in old stands. Roosting opportunities in the forest appear to be limited, however, in that several roost characteristics selected by bats were of low availability even in old forests, yet individual bats appear to require several roost trees. Therefore, roost site location may be the sole determinant of the stand ages selected by bats. Differences in abundance and foraging activity may be the consequence of this roost selection. Others have also suggested that roosts determine

foraging habitat (e.g. Kunz 1982, Furlonger et al. 1987). Foraging in old stands may occur only incidentally as bats move to and from roosts. The reduced clutter of old stands simply makes foraging *en route* easier and more profitable than in other ages. Recent observations support this hypothesis as many bats commute long distances from suitable roost sites to foraging sites (Brigham 1991, de Jong 1994).

Bats could be selecting old stands for their improved foraging opportunities, particularly in terms of reduced clutter (Lee et al. 1995a). However, differences in foraging opportunities among stand ages were less striking than differences in roosting opportunities, in that even in young stands some gaps, but no roost trees, were found. Therefore, a more likely explanation is that bats select old stands as the best combination of both roosting and foraging opportunities. In particular, during certain periods, it seems likely that old stands satisfy both roosting and foraging needs, if, as in northern Sweden (de Jong in press), insect densities are high within the forest in the middle of the summer. At this time, pregnant and lactating bats are less likely to fly long distances, as supported by my radiotelemetry observations. The relative importance of old stands as foraging habitat may therefore be seasonal in nature. Until we assess what use bats can make of areas other than old stands for foraging, the distribution of insect prey in the forest, and what foraging rates are adequate, the importance of foraging habitat selection in determining the preference of bats for older stands is unclear. The experimental manipulations of roosting and foraging opportunities in the aspen mixedwood forest, presented in Chapter 3, may help clarify this issue.

CHAPTER 3

EFFECTS OF FRAGMENTATION ON BAT ABUNDANCE AND ACTIVITY IN ASPEN MIXEDWOOD STANDS

Introduction

A major agent of change in natural systems is disturbance, which often interrupts habitat continuity, and may initiate younger seral stages. Historically, disturbances such as fire have shaped landscapes, creating patches of habitat that differ in age, size, shape, and composition. Increasingly, anthropogenic disturbances such as agriculture and forestry are assuming this role, leaving a reduced total area of some natural habitats, in smaller and more isolated fragments. In particular, older primary forest is being depleted rapidly by these agents, and is being replaced by a mosaic of cut areas, younger forests, and regrowth forests (Chen and Franklin 1992, Zubaid 1993) that may differ in composition from primary forests (Carey and Johnson 1995, Lee et al. 1995a)

Changes in the diversity and abundance of species following forest fragmentation may result from three factors (Andren 1994, Andren and Delin 1994). The loss of total area of original habitat may lead to a decrease in some of the resources available to resident species, and an increase in those available to colonizing species. Smaller fragment size, and increased distance between habitat patches after fragmentation may also lead to a decline in biological diversity (Andren 1994), as predicted by island biogeography theory (MacArthur and Wilson 1967). The importance of these three factors may vary according to the degree of fragmentation (Andren 1994). Additionally, forest fragmentation creates more edge habitat, which may have consequences for the organisms remaining in the patches (Murcia 1995). The response of populations or communities to fragmentation may depend, therefore, on the scale and pattern of fragmentation; organisms in large patches may be less affected than those in small isolated patches. In forest systems, fragmentation also has a temporal component. The

effects of fragmentation cannot only be examined as the difference between forested and non-forested areas; the replacement of older natural forests with younger managed forests that may differ in composition due to differences in the nature of the disturbance (Lee et al. 1995a) must also be considered.

The effect of forest fragmentation also is influenced by the ecology of a given species or community; while some species may experience a loss of resources, others may experience a gain. Additionally, some species may be more sensitive to size and isolation than others. Some species flourish in cut blocks (e.g. Pine Siskins *Carduelis pinus*: Keller and Anderson 1992; aerial insectivorous birds: Franzreb and Omhart 1978; wintering and breeding birds: Yahner 1993) or younger forests (moose: *Alces alces* Peterson and Peterson 1992). Others, however, decline in cut blocks (e.g. cavity nesting birds: Franzreb and Omhart 1978; canopy or insectivorous birds: Thiollay 1992; woodland caribou *Rangifer tarandus*: Chubbs et al. 1993; red squirrel *Sciurus vulgaris*: Andren and Delin 1994, Wauters et al. 1994), or depend on old forests (e.g. Red-cockaded woodpecker *Picoides borealis*: Rudolph and Conner 1994). These differences in response reflect differences among species in food resources (Keller and Anderson 1992), foraging behaviour (Franzreb and Omhart 1978), need for cover, and nesting/denning/roosting requirements. For example, some insects take advantage of the new flush of vegetation in cutblocks and numbers increase (Murcia 1995). On the other hand, many cavity nesters depend on old stands for large, decaying nest trees and may decrease in number after logging (Stelfox 1988, Rudolph and Conner 1994).

The response of bats to forest fragmentation has not been well documented. Bats use forests (Jones et al. in press, Kalcounis and Brigham 1995) and forest edges (Leonard and Fenton 1983, Racey and Swift 1985, Barclay 1985, de Jong and Ahlen 1991) for foraging and roosting (Taylor and Savva 1988, Lunney et al. 1988, Vonhof 1995), and have been associated with older (Stelfox 1988, Thomas 1988, Perkins and Cross 1988),

and primary (Lunney et al. 1988, Taylor and Savva 1988, Zubaid 1993) forests. Habitat requirements of bats include aspects of roosting and foraging, and habitat preferences may reflect a combination of the two (Furlonger et al. 1987, Taylor and Savva 1988). Fragmentation may affect the amounts of both roosting and foraging habitat available to bats, and thus may influence bat abundance.

For many insectivorous bats, fragmentation initially may improve foraging habitat, in that it reduces the amount of clutter presented to foraging bats. Habitat use in some species is thought to be constrained by wing and echolocation call design, which make these species less maneuverable and less tolerant of echoes (Aldridge and Rautenbach 1987, Norberg and Rayner 1987). Additionally, prey abundance may be greater in cutblocks, particularly along edges (Lewis 1970). On the other hand, prey composition may change in cut areas, and may not include preferred items. Moreover, bats may be more vulnerable to predation in open cut areas; thus, isolation of fragments may exacerbate the effects of the changes to original habitat.

Fragmentation is likely to have a negative impact on roosting habitat of bats, in that the loss of older forests reduces the number of large trees, especially snags (Stelfox 1988, Ohmann et al. 1994). Trees and snags left standing after harvest, including those in remnant patches, are more subject to blow down (Williams-Linera 1990, Chen and Franklin 1992, Allen 1993). The loss of these trees may affect populations of mammals that use tree-cavities (Zarnowitz and Manuwal 1985). Some bats preferentially roost in large diameter trees (Barclay et al. 1988) and often in cavities (see Chapter 2; these trees may be unavailable in logged and regrowth forest (Taylor and Savva 1988). Harvesting may have long term consequences for roost trees as managed forests are impoverished in large trees and snags (Evans and Connor 1979, Cline et al. 1980, Mannan et al. 1980), especially cavity trees (Healy et al. 1989).

Forest fragmentation in the aspen mixedwood forest of Alberta will introduce a new disturbance regime that is predicted to reduce the proportion of old forests in the region (Stelfox 1995). Also, the disturbed areas will resemble, but will not be identical to, the areas left after the traditional disturbance, fire. The effects of this fragmentation on insectivorous bat populations may result from a combination of the predicted negative impacts on availability of roost trees, and possible improvements to foraging habitat. Determining the overall effects may help elucidate the relative importance of roost site and foraging habitat selection in determining bat distributions. Experimental harvesting in the aspen mixedwood forest has created the unusual opportunity to study these effects by comparing bat abundances in the same stands pre- and post-fragmentation. I thus set out to determine if bat abundance and activity in the aspen mixedwood forest changed immediately following forest fragmentation; longer-term consequences will need to be investigated. For the short term, at the stand level, I expected that there would be a decrease in bat abundance in fragmented stands. I based this expectation on three predictions:

Prediction 1: Forest edges are preferred foraging habitat for insectivorous bats (Leonard and Fenton 1983; Barclay 1985; Swift and Racey 1985; Rydell 1986, 1989b; Furlonger et al. 1987; Krull et al. 1991; de Jong 1994, Grindal 1995). Therefore, I predicted that bat activity would be greater along the edges of logged sites than within unlogged forest or other parts of the cutblocks.

Prediction 2: The increase in foraging activity along edges likely translates into increased activity in logged sites compared to unlogged sites, although a loss of roost trees may reduce activity.

Prediction 3: However, the loss of roost trees from the stand as a whole, and consequent depletion of the bat population outweighs the increase in foraging activity in logged sites, and bat abundance decreases in remaining unlogged patches.

Methods and Materials

Between 18 May and 22 August in both 1993 and 1994, I sampled bat abundance and activity in two unfragmented (control) and two (to be) fragmented stands in each of mature (50-65 years) and old (>120 years) forests (four stands per age). Fragmentation, in which 95% of the trees were removed from 30-40 ha plots within stands, occurred in the winter of 1993-94. In unfragmented stands of each age, I monitored activity in a total of 11 and 12 sites in 1993 and 1994, respectively. In fragmented stands, I sampled bat abundance and activity in six (to be) logged and six unlogged sites per age in each year. I randomized site sampling order among ages and treatments, but ensured that I monitored one logged site per week, alternating between mature and old sites. Each night, I monitored one site, using two methods: mistnetting and echolocation-call monitoring (see Chapter 1 for details).

In unlogged sites, I placed nets and monitored bat passes and buzzes along a transect as described in Chapter 2. In logged sites in 1994, I sampled three habitats: centre of the cutblock, edge of the cutblock, and forest surrounding the cutblock. I located the site centre (now in the clear cut), and identified the nearest edge; if two edges were equidistant, I chose the lee edge. Edges were 100-250 m from cutblock-centre monitoring positions. I then measured a distance of 50 m into the forest (perpendicular to the edge) and established a sampling position.

I used one to three mist nets each night in logged sites. In general, all nets were placed along and perpendicular to the edge, on small hummocks, or between residual clumps of trees. However, on two occasions, nets were set over small creeks, once in the forest, and once in the cutblock centre. I set nets to approximately 6 m in height no later than 15 minutes after sunset, for approximately 120-150 minutes.

In logged sites, I monitored echolocation passes and buzzes at the centre of the cutblock for 20 minutes, while my assistant monitored activity at the forest monitoring

position. We then monitored at the edge for 20 minutes before returning to our original positions. This cycle continued for the two hour monitoring period (beginning 15 minutes after sunset). Both detector frequencies (25 and 40 kHz) were monitored at all times. In half the sites in each age, we started the monitoring cycle at the edge, and in the other half, in the centre/forest. Also, a given observer alternated between monitoring the centre and the forest among sites.

This monitoring program allowed me to evaluate how bats use disturbed areas on several levels. First, within logged sites, I compared relative activity, including foraging activity and effort (the ratio of feeding buzzes to passes) in the different habitats (cutblock centre, edge, forest) to determine if bats preferred certain areas of logged sites (prediction 1). Within fragmented stands, I compared relative activity between logged and unlogged sites to evaluate the effect on bat activity of removal of trees at the site level (prediction 2). I also compared relative activity in unlogged sites in fragmented stands to that of unfragmented stands to assess the effects of fragmentation on bat activity at the stand level (prediction 3).

Statistical Analyses

The effect of fragmentation on activity in logged sites and fragmented stands should be viewed in the context of the general increase in bat activity from 1993 to 1994 (Chapter 2). In all analyses of the effect of treatment, I first had to control for year-to-year differences. Therefore, I compared the magnitude and direction of the change, in number of captures or passes, from 1993 to 1994, between treatments. In other words, fragmentation had an effect on bat activity only if the amount of the change in treated sites from 1993 to 1994 was greater than, or in the opposite direction to, that of control sites.

To determine the effect of treatment on the number of captures, I compared the actual number of captures in the two years (1993 = control) to the expected number of

captures (based on number of net nights/year) using chi-squared tests. I conducted these tests on logged, unlogged and unfragmented sites separately. I compared the result from treated sites to that of control sites within each age to distinguish year effects from treatment effects. I used only sites that had been sampled in both years.

In comparisons of echolocation activity among treatments, I used only sites that had been sampled in both years. I analysed activity in hour 1 and hour 2 separately, based on the difference in activity in these two hours reported in Chapter 2. I also analysed mature and old stands separately, as I did not have sufficient replication to use Analysis of Variance (ANOVA) models with age as an additional main effect. As activity data were not normally distributed, I transformed (usually log-transformation, but sometimes inverse- or square root-transformation) them before conducting ANOVAs. When possible, I analysed total bat activity (the number of passes detected for all bat species combined), *Myotis* spp., and *L. noctivagans* activity in both ages and hours. However, in some cases, transformations could not normalise the data, or there were insufficent data. To compare logged sites and fragmented stands to controls, I therefore also employed Mann-Whitney tests where possible.

Use of different habitats within logged sites

To determine if bats preferred certain habitats within logged sites, I compared bat activity (passes/hour) in the different habitats in 1994 with two-way ANOVA, with stand and habitat as main effects. I used inverse-transformed data in all cases, except old stands in hour 2. I used Tukey's tests to determine which habitat means differed significantly.

Activity in logged and unlogged sites

I compared activity between logged and unlogged sites within fragmented stands using two-way ANOVA, with year and site-treatment as main effects, and site as a nested

effect. The interaction term indicated whether site treatment affected bat activity between 1993 and 1994. For each age and hour, I conducted the analysis twice, using different values to represent logged sites: the number of passes detected at the edge, and the number detected at the centre of the clearcut. In some cases, I used Mann-Whitney tests to compare the effect of logging on the difference in activity between years (on *Myotis* activity in all cases except old stands hour 1; *L. noctivagans* activity when centre was used, in all cases except old stands, hour 1).

Activity in fragmented and unfragmented stands

I compared bats' use of unlogged sites in fragmented stands to that of sites in unfragmented stands with two-way ANOVA, with year and stand treatment as main effects, and site as a nested effect. The interaction indicated whether stand treatment affected bat activity. In some cases I used Mann-Whitney tests to compare the effect of fragmentation on the difference in activity between years (on *Myotis* activity in all cases except old stands hour 1; *L. noctivagans* activity in old stands, hour 2 and mature stands, hour 1).

Foraging activity

To analyse differences in foraging activity among the different treatments and between the two years, I used chi-squared tests on the number of total and *Myotis* buzzes detected in old stands. To compare foraging among treatments and years in mature stands, I used randomisation tests on total and *Myotis* buzzes.

For echolocation activity results, I report means and standard errors, based on the appropriate back-transformation from ANOVAs. For this reason, standard errors are asymmetrical. I report medians and quartiles from Mann-Whitney tests. For captures

and foraging activity, I report total numbers of captures and buzzes, respectively. I used $\alpha=0.05$ as the level of significance in all tests.

Results

After differences in sampling effort were standardised, in 1993 and 1994 respectively, I detected a total of 213 and 264 passes in logged sites, 222 and 194 passes in unlogged sites in fragmented stands, and 684 and 1072 passes in control sites. I detected *Myotis* spp., *Lasionycteris noctivagans*, *Lasiurus cinereus*, and *Eptesicus fuscus* in both logged and unlogged sites, including unlogged sites in unfragmented stands. *Myotis* spp. activity was greater than that of other species in all cases; in 1993, it accounted for 80% of total activity, and in 1994, 70% (treated and control sites combined). Similar percentages were found for each year within logged, fragmented and control sites. *L. cinereus* and *E. fuscus* were only detected at low levels, and were not captured in any sites. Captures within sites were exclusively *Myotis lucifugus* (40/47 bats over two years) and *L. noctivagans* (n=7).

In 1993, most bats (10/19) were captured in unfragmented old stands; in 1994, most bats were captured in logged mature stands (20/28) (Table 3.1). There were too few captures in most treatments to analyse differences between the two years with two exceptions. In mature stands, more bats were captured after logging than before ($\chi^2=15.09$; df=1; $P < 0.001$; Figure 3.1a). It appeared (although numbers were low), that there was no concurrent increase in unfragmented stands. In old stands, there was a decrease in the number of bats caught in unfragmented stands, however, from 10 bats in 1993, to 1 bat in 1994 ($\chi^2=13.7$; df=1; $P < 0.001$; Figure 3.1b). The ten bats caught in 1993 were all from one site; in 1994, we netted successfully at that site prior to site sampling (for radiotelemetry), and may have deterred bats, thus reducing the number of captures. Thus this decrease may not reflect an actual decline in the population in old unfragmented stands.

Table 3.1. Numbers of bats captured in logged and unlogged sites in fragmented stands, and in control sites in unfragmented stands, in mature and old aspen mixedwood forests, 1993 and 1994. In 1993, no sites had been logged.

Stand Age	Bat Age	Sex	1993			1994		
			Logged	Unlogged	Unfrag-mented	Logged	Unlogged	Unfrag-mented
Mature	Adult	Female	0	2	0	16	0	0
	Adult	Male	0	1	0	1	0	0
	Juv.	Female	0	0	1	2	1	0
	Juv.	Male	0	1	1	1	0	0
		Total	0	4	2	20	1	0
	# net nights		9	10	0	0	11	0
Old	Adult	Female	1	0	5	0	3	0
	Adult	Male	0	0	2	0	0	0
	Juv.	Female	1	1	3	1	0	1
	Juv.	Male	0	0	0	1	1	0
		Total	2	1	10	2	4	1
	# net nights		14	11	27	12	11	46
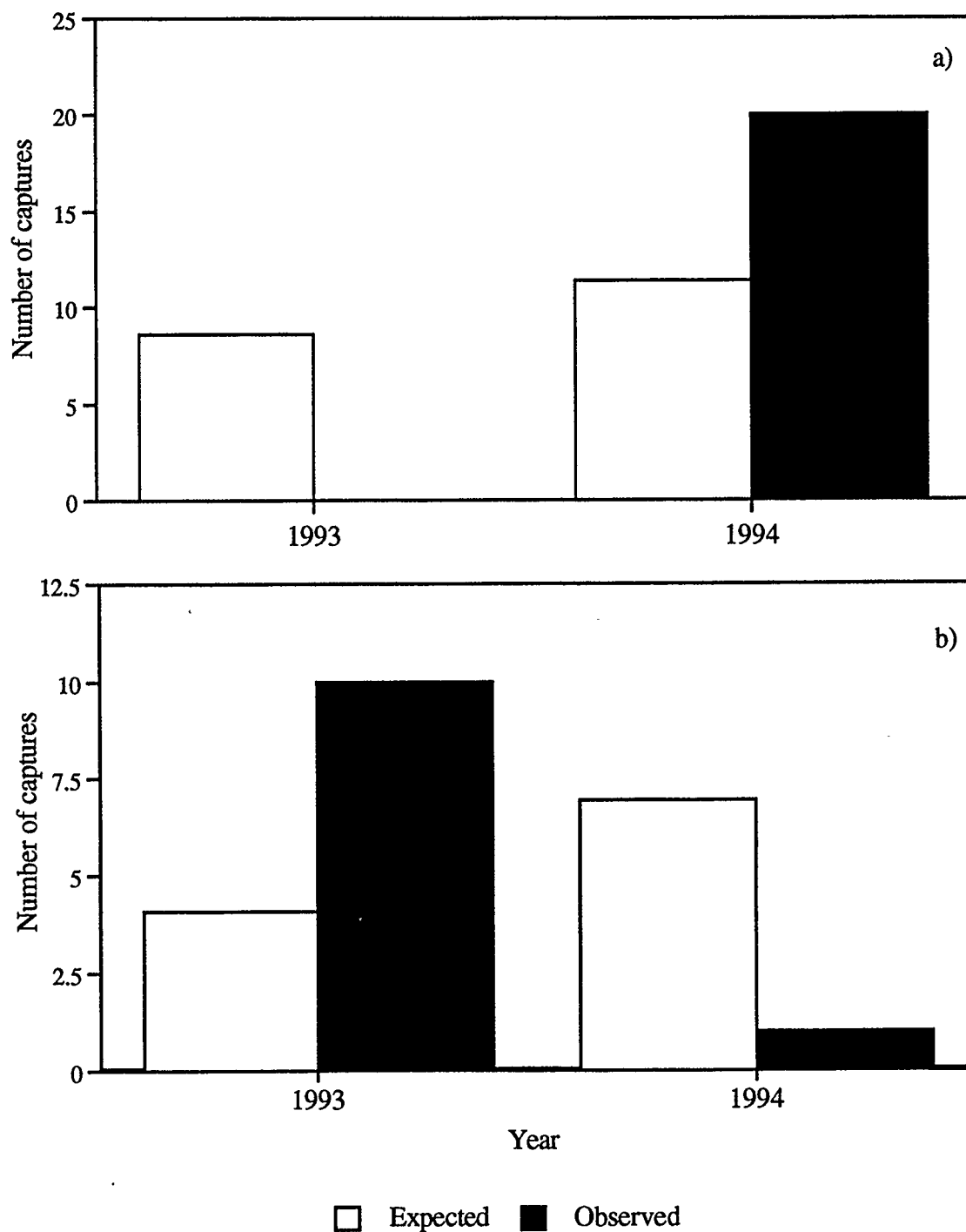
Figure 3.1. Total number of observed and expected (based on sampling effort) captures in a) logged sites in fragmented mature stands, and in b) control sites in unfragmented old stands, in aspen mixedwood forests in 1993 and 1994. No sites had been logged in 1993. Mature: 1993 n=9, 1994 n=12 net nights; Old: 1993 n=27, 1994 n=46 net nights.

Use of different habitats within logged sites

In logged sites, bats appeared to prefer the edge habitat in both mature (Figure 3.2) and old stands, followed by centre, then forest. I could not draw any statistical conclusions for old stands in hour 1; given the low numbers of bats detected in the forest and the centre, activity was not normally distributed within these classes. Total bat activity in old stands in hour 2 did not significantly differ among habitats (F=1.02; df=2,14; $P > 0.25$), although mean activity on the edge (3.07 passes/20 min) appeared greater than mean activity in the forest (1.03 passes/20 min) or centre (0.79 passes/20 min). In mature stands in both hours, however, activity among habitats differed significantly (hour 1: F=5.07; df=2,14; $P < 0.025$; hour 2: F =5.62; df=2,14; $P < 0.025$; Figure 3.2a and b). Bats were more active along the edge (hour 1: 5.71 passes/20 min, hour 2: 2.37 passes/20 min) than in the forest (0.41 passes/20 min in hour 1, 0.24 passes/20 min in hour 2). Mean activity in the centre (0.66 passes/20 min in hour 1, 1.08 passes/20 min in hour 2) did not significantly differ from either of the other two habitats.

Analyses of *Myotis* activity in hour 1 were hampered by the fact that there was no variance within some classes because no bats were detected in the centre (old, hour 1) or forest (mature, hour 1) of any sites in a given stand. The trend in these cases was for greatest activity along the edge. In hour 2 in both mature and old stands, there was no significant difference in *Myotis* activity among habitats. In mature stands, mean activity was 1.31, 0.71, and 0.24 passes/h at the edge, centre and forest, respectively (F=1.83; df=2,14; $P > 0.1$). In old stands, mean activity was 0.61, 0.39, and 0.29 passes/h, at the edge, centre and forest respectively (F= 0.42; df=2,14; $P > 0.5$).

Activity in logged and unlogged sites

In general, logging had no effect on bat activity in either forest age or either hour. Changes in total bat activity in logged sites from 1993 to 1994 were not significantly different than changes in activity in unlogged sites, regardless of the habitat used as the
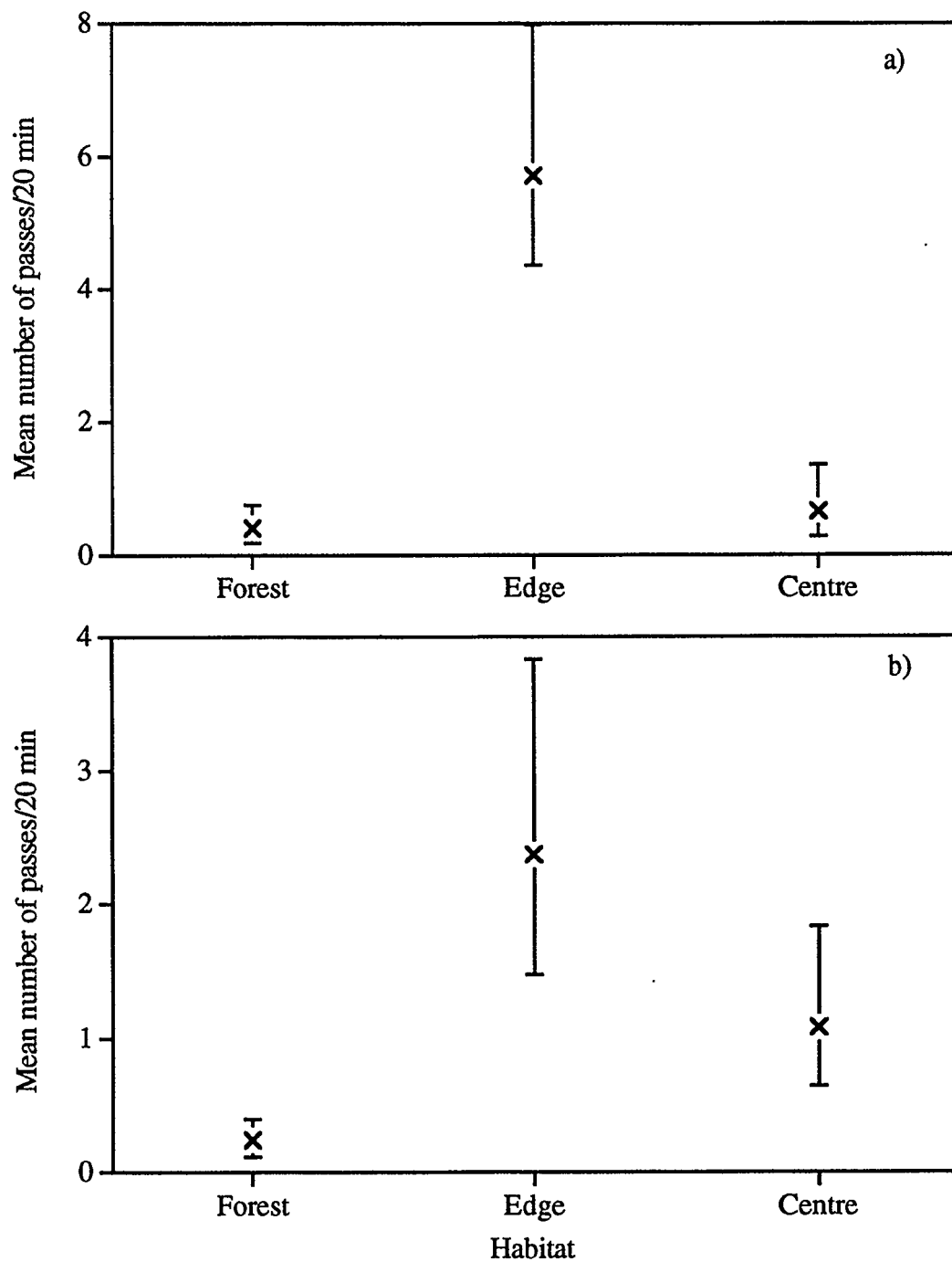
Figure 3.2. Mean (± S.E.) number of passes/20 minutes detected in different habitats of logged sites in mature aspen mixedwood stands, 1994. a) hour 1, b) hour 2. Means and S.E.'s were calculated from inverse-transformed data, thus S.E.'s are asymmetrical. n=6 sites/habitat.

value for logged sites. However, there was a general trend of increased activity (relative to unlogged sites) in logged sites when edge was used in the comparison, and decreased activity in logged sites when cutblock centre was used. For example, in old stands in hour 1, when I used centre, mean activity increased marginally in intact sites and remained constant in logged sites, but the difference in the changes between unlogged and logged sites was not significant (F =0.79; df=1,10; P > 0.25; Figure 3.3a). When I used edge activity in the comparison, there was a non-significant relative increase in activity in logged sites compared to unlogged sites (F =3.23; df=1,10; P > 0.05; Figure 3.3b). There was similarly no relative difference following logging in old and mature stands in hour 2, in either habitat, although they followed the same pattern. In mature stands in hour 1, however, there was a significant increase in total bat activity on the edge after logging, compared to unlogged sites (F = 6.44; df=1,10; P < 0.05; Figure 3.4a). Mean activity on the edge increased from 4.5 passes/h in 1993 to 21.7 passes/h in 1994.

The same general and usually non-significant trends were observed for *Myotis* activity. However, in old stands in hour 1, the decrease in mean *Myotis* activity in the centre of logged sites (from 1.97 passes/h in 1993 to 0 passes/h in 1994) differed significantly from the increase (from 3.39 passes/h to 7.58 passes/h) in activity in unlogged sites (F = 5.11; df=1,10; P < 0.05; Figure 3.5a). There was no significant change from 1993 to 1994 in mean *Myotis* activity when edge activity in these logged sites was compared to that of unlogged sites (Figure 3.5b). Mann-Whitney tests were used for all other comparisons, with the same general results. Only one case was significant: there was a relative increase in activity along the edge of logged sites in old stands in hour 2 (median difference: unlogged sites=0.0, logged sites=2.0 passes/h; U = 32; n_1 = 6, n_2 = 6; P < 0.05).

There were no significant differences in *L. noctivagans* activity between either the centre or the edge of logged sites, and unlogged sites in old or mature stands in either
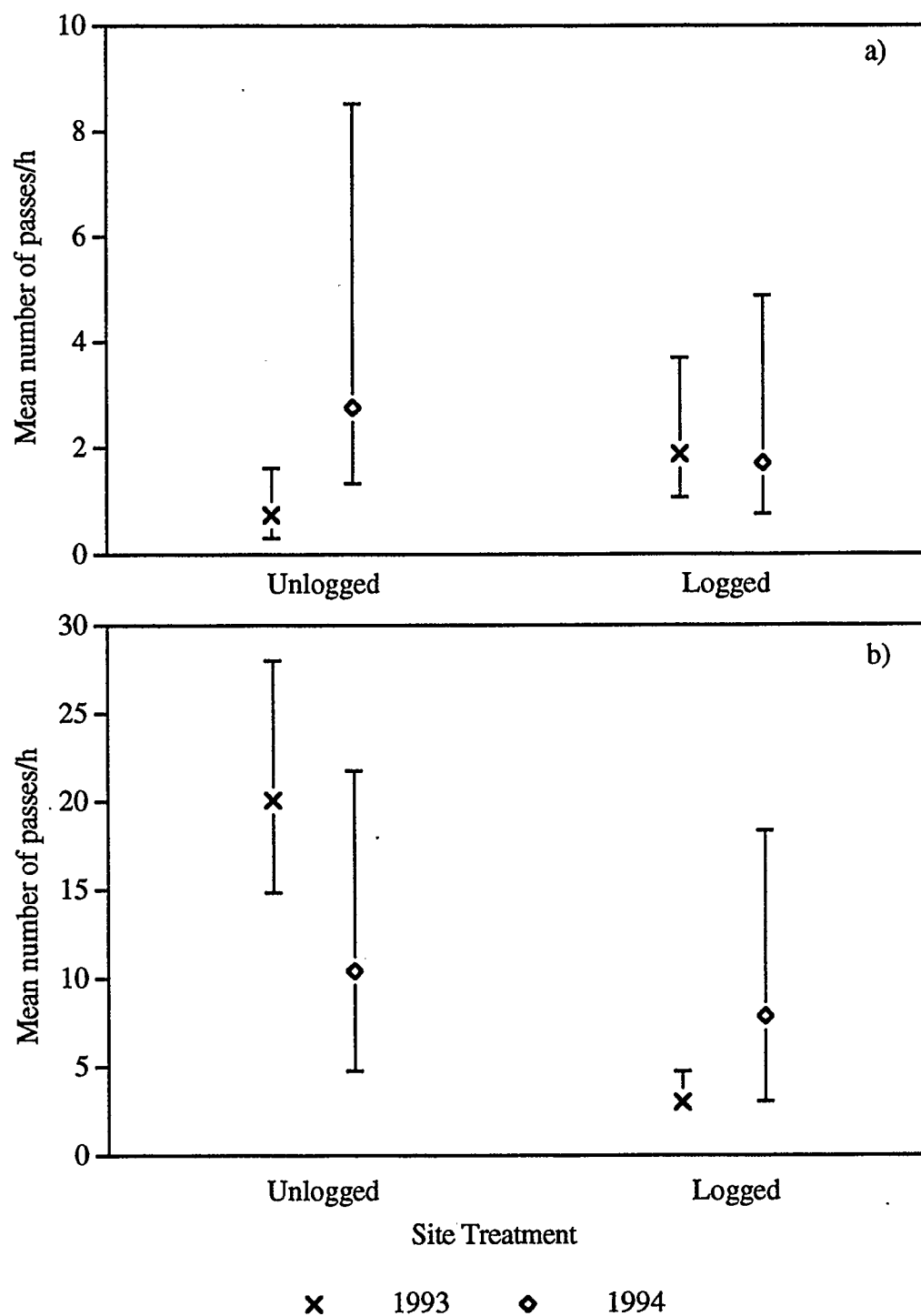
Figure 3.3. Mean (± S.E.) number of total passes/h detected in unlogged sites, and in the a) centre and b) edge of logged sites, in old aspen mixedwood fragmented stands in hour 1 in 1993 and 1994. In 1993, sites had not yet been logged. Means and S.E.'s were calculated from a) inverse- and b) log-transformed data, thus S.E.'s are asymetrical. n=6 sites/treatment/year.
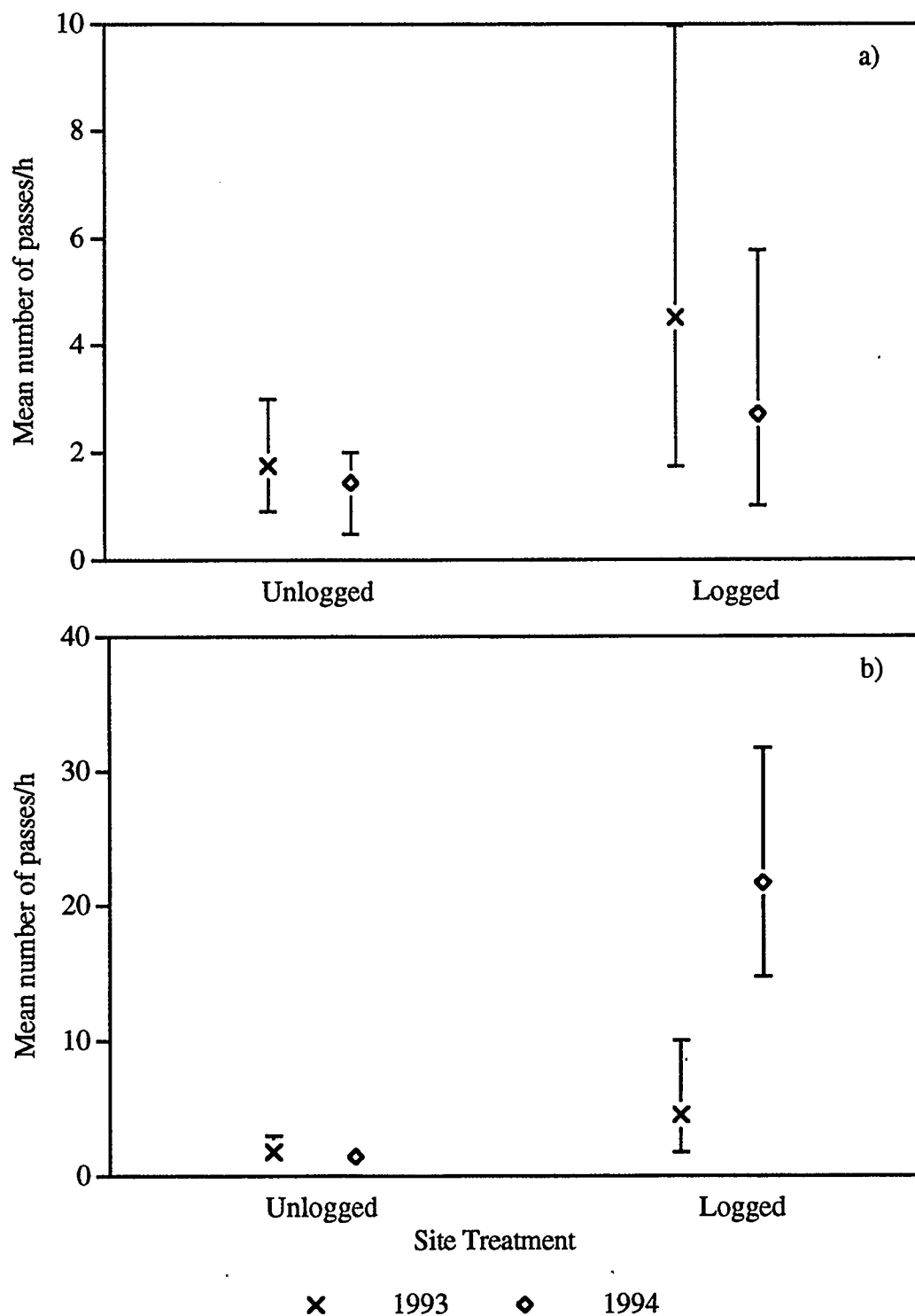
Figure 3.4. Mean (± S.E.) number of total passes/h detected in unlogged sites, and in the a) centre and b) edge of logged sites in fragmented mature aspen mixedwood stands in hour 1 in 1993 and 1994. In 1993, sites had not yet been logged. Means and S.E.'s were calculated from log-transformed data, thus S.E.'s are asymmetrical. n=6 sites/treatment/year.
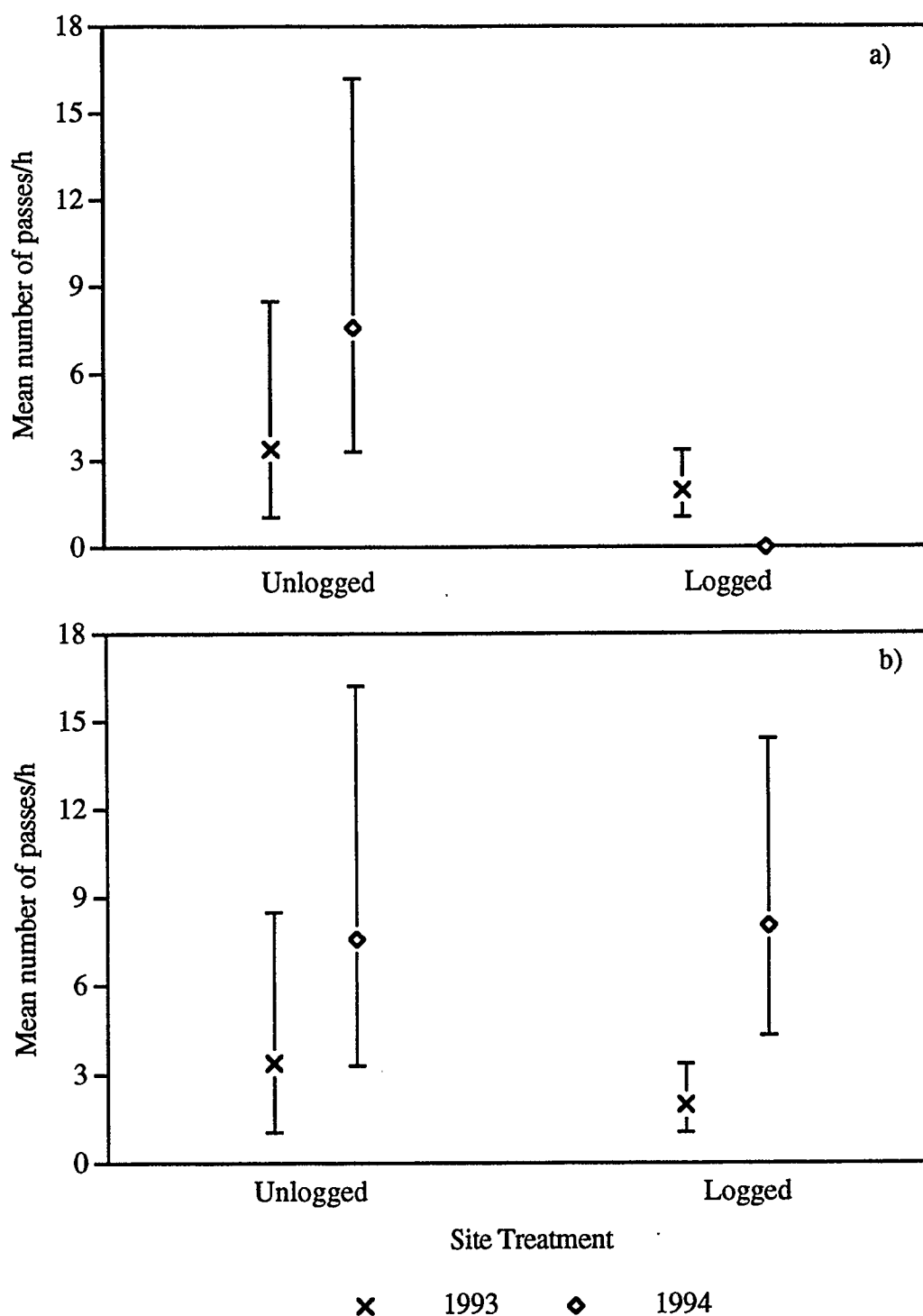
Figure 3.5. Mean (± S.E.) number of *Myotis* spp. passes/h detected in unlogged sites, and in the a) centre and b) edge of logged sites, in old aspen mixedwood fragmented stands in hour 1 in 1993 and 1994. In 1993, sites had not yet been logged. Means and S.E.'s were calculated from log-transformed data, thus S.E.'s are asymmetrical. n=6 sites/treatment/year.

hour (I used Mann-Whitney tests on all centre-based comparisons). There were no changes in mean activity over the two years in either the treatment or control stands; *L. noctivagans* activity was low in all stands in both years, ranging from 0.03 passes/h to 1.72 passes/h.

Activity in fragmented and unfragmented stands

Activity following fragmentation was eithr reduced, although not significantly, or remained unchanged compared to activity in unfragmented stands. In general, there was a tendency for activity in control stands to increase more than in fragmented stands from 1993 to 1994. The general trend is illustrated in Figure 3.6a; in old stands in hour 1, mean total activity increased from 15.0 passes/h to 39.0 passes/h in unfragmented stands, and from 7.83 passes/h to 10.4 passes/h in fragmented stands. In two cases in old stands (total activity in hour 2, *L. noctivagans* in hour 1), activity decreased in fragmented stands while increasing in unfragmented stands. Total activity in mature stands in hour 1 showed a slightly different pattern from the other species and ages, in that it decreased slightly in both control and fragmented stands (Figure 3.6b).

Foraging activity

In mature stands, I heard a total of 23 buzzes in 1993 and 27 buzzes in 1994 in all sites combined. In both years, the majority of buzzes were heard in (to be) logged sites (1993: 16 buzzes, 1994: 22 buzzes). In 1994, at these logged sites, no foraging buzzes were heard in the forest; all but one were detected at the edge. In old stands, I heard a total of 78 buzzes in 1993, the majority (72 buzzes) in control sites, and 216 buzzes in 1994, the majority (143 buzzes) in fragmented sites. In 1994, at logged old sites, one third (total n = 12 buzzes) of the foraging buzzes (all *Myotis* spp.) were detected in the forest; the rest were detected on the edge.
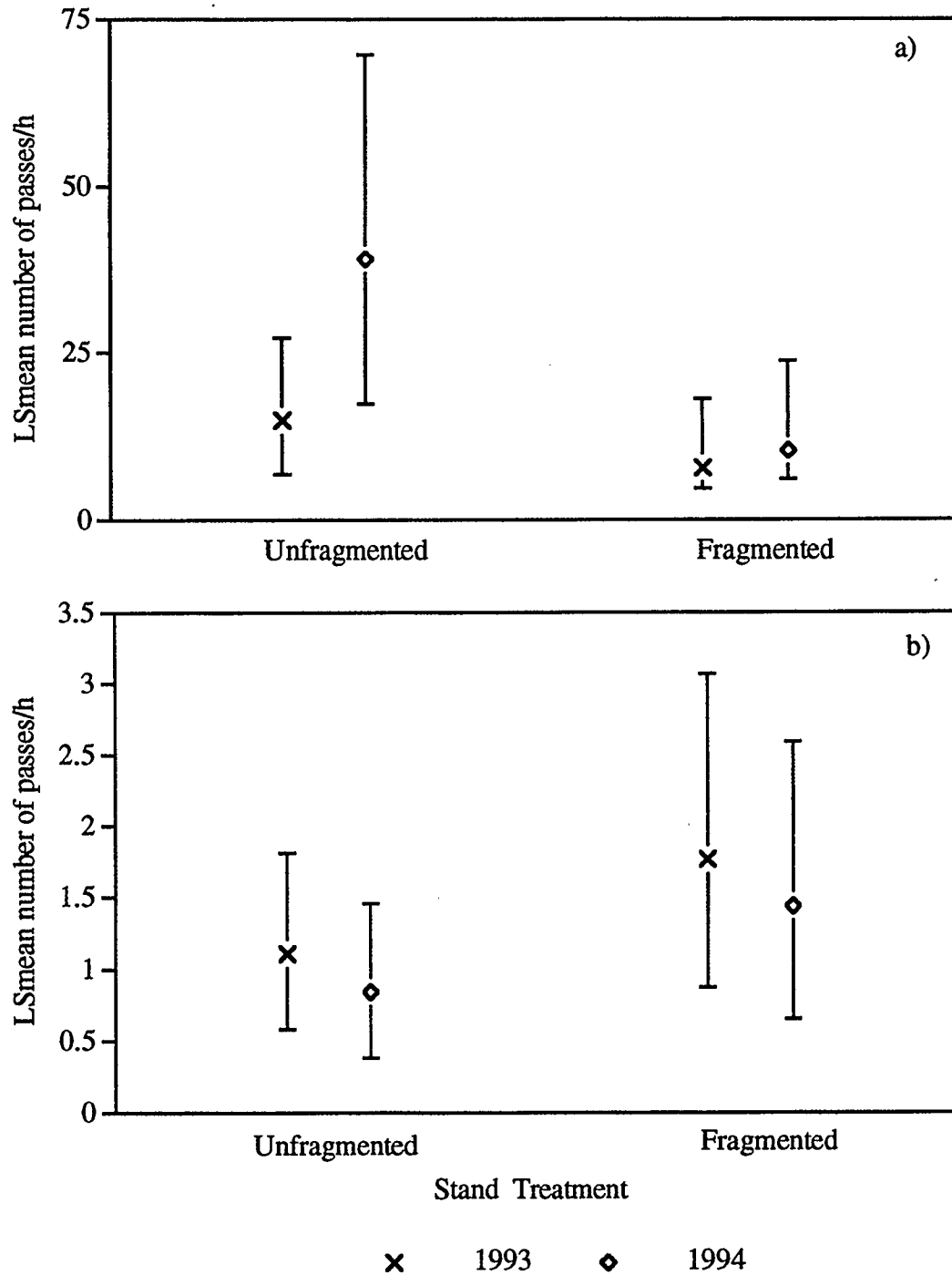
Figure 3.6. Least Squares Mean (± S.E.) number of total passes/h detected in unfragmented and fragmented a) old and b) mature aspen mixedwood stands in hour 1 in 1993 and 1994. In 1993, fragmented stands had not yet been logged. Means and S.E.'s were calculated from log-transformed values and thus S.E.'s are asymmetrical. Unfragmented: n=11, Fragmented: n=6 sites/year. There were two stands in each treatment; in fragmented stands, only the unlogged sites were included.

Total foraging activity in mature stands did not differ significantly between years in any treatment (randomisation test: $G = 2.16$, $P > 0.25$; Figure 3.7a). In old stands, the distribution of feeding buzzes was influenced by year ($\chi^2 = 17.4$; df=2; $P < 0.001$; Figure 3.8a). Specifically, I observed higher than expected foraging activity in logged sites and fragmented sites in 1994, and lower than expected activity in logged sites in 1993. *Myotis* foraging activity followed the same patterns. In mature stands there was no difference between years or among treatments (randomisation test: $G = 2.34$, $P = 0.50$; Figure 3.7b). However, in old stands, *Myotis* foraging activity was influenced by year in the same manner as total activity ($\chi^2 = 15.89$; df=2; $P < 0.001$; Figure 3.8b).

When total foraging effort (the ratio of buzzes to passes) was examined, there was a slight increase in logged sites in both mature and old stands from 1993 to 1994, a decrease in all fragmented stands, and old unfragmented stands, and no change in mature unfragmented stands (Table 3.2). These results indicate that, in proportion to their activity, bats forage relatively more in sites after logging. *Myotis* foraging effort increased in all cases except old unfragmented stands, where it decreased. The increases reflected an absence of *Myotis* foraging activity in many sites in 1993.

Discussion

Any changes in bat abundances in forests following fragmentation will reflect the combined impact of harvesting on roosting and foraging habitat. This impact is manifested at different levels within fragmented stands. By examining the habitat choices made by flying bats within logged sites, the effect on foraging habitat can be examined. On the other hand, comparisons of intact portions of fragmented stands with unfragmented stands help clarify the impact on roosting habitat.

I predicted that fragmentation would increase foraging and commuting habitat through the creation of edges. Within logged sites, I found that bats generally preferred the edge of cutblocks to the forest or the centre of clearcuts, particularly in hour 1 when
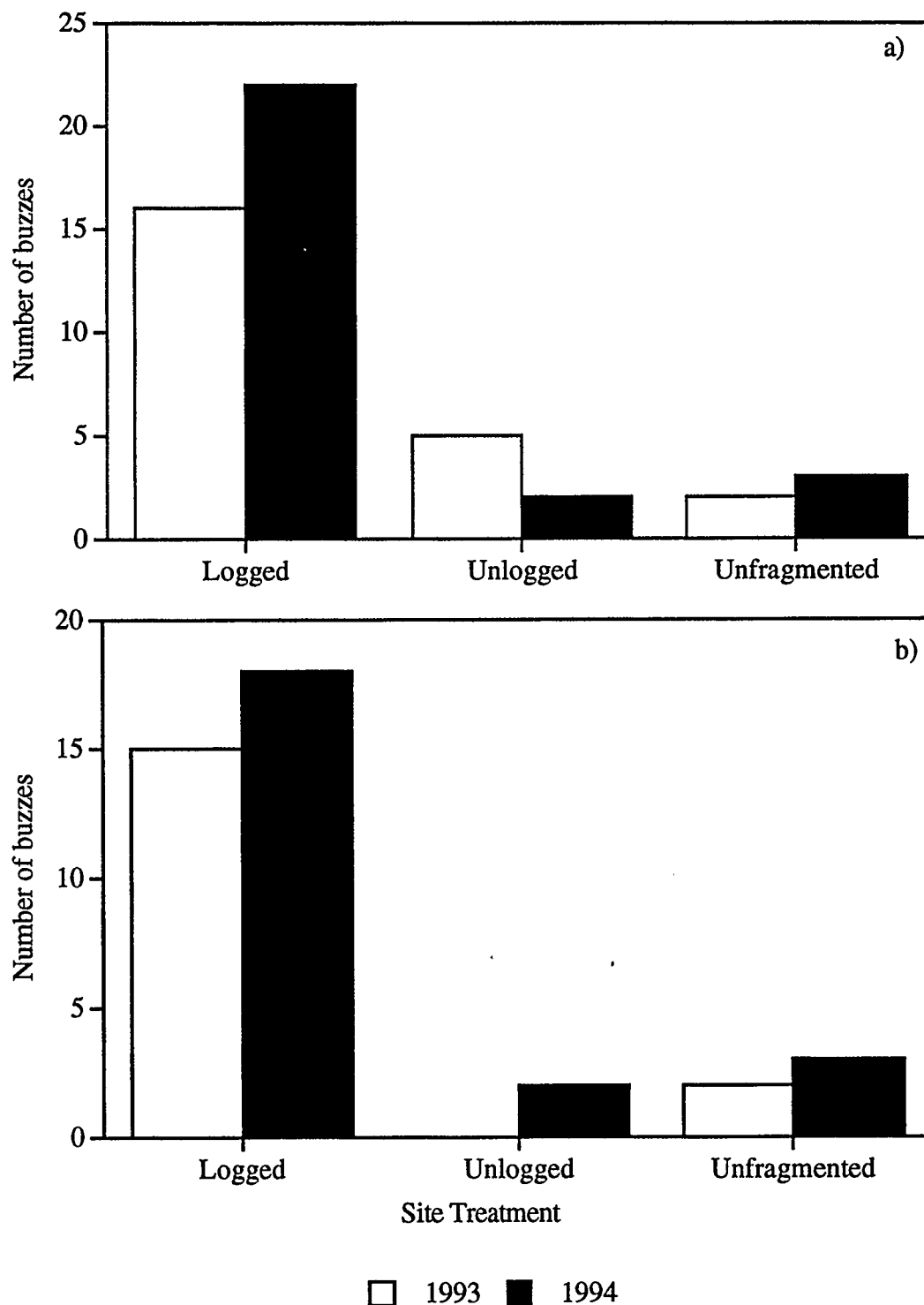
Figure 3.7. Total number of foraging buzzes detected in logged and unlogged
sites in fragmented stands, and control sites in unfragmented stands, in mature
aspen mixedwood forests in 1993 and 1994. In 1993, no sites had been logged.
a) Total bats, b) *Myotis* spp. n=6 sites/treatment/year in fragmented stands,
and 11 sites/treatment/year in unfragmented stands.
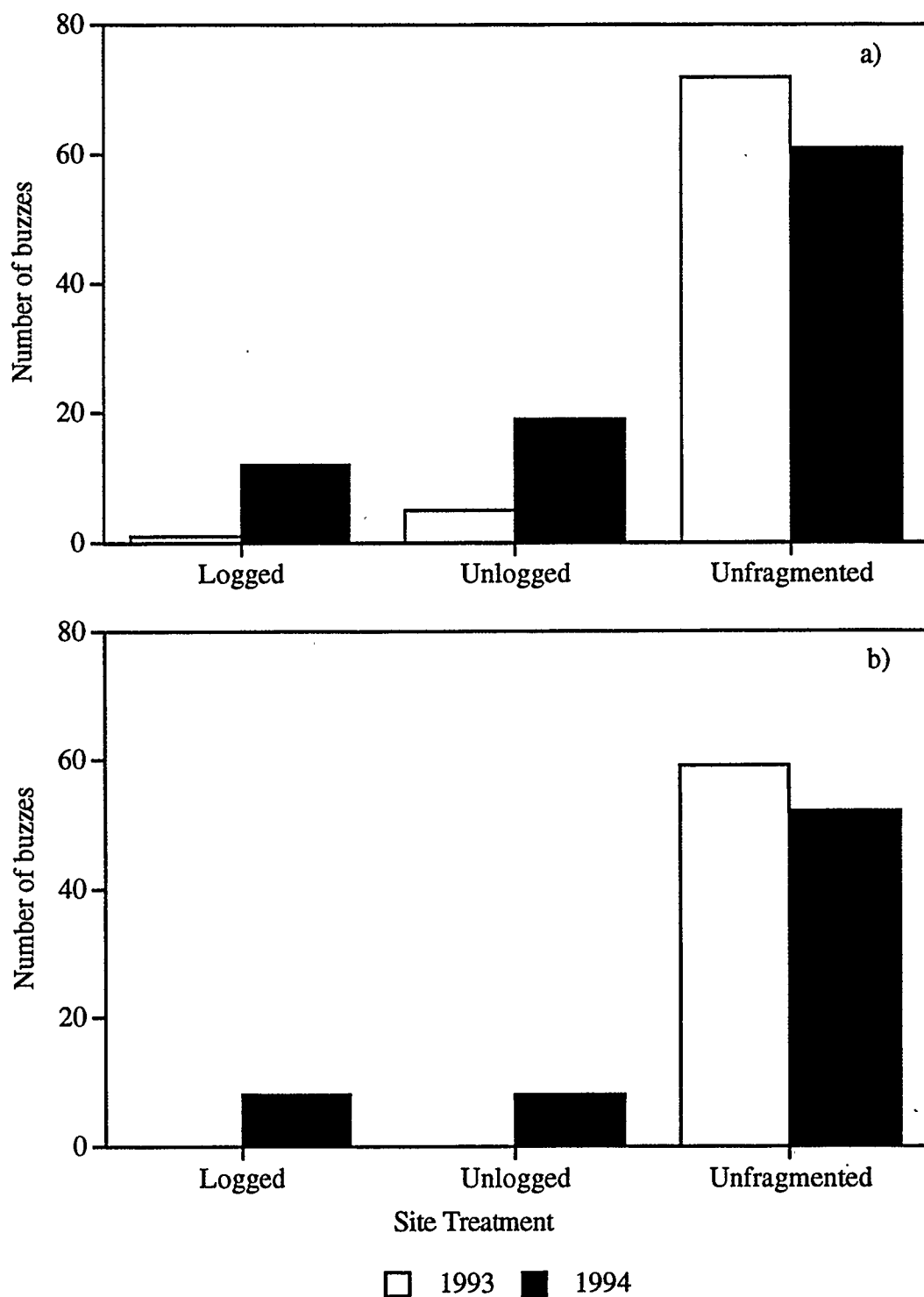
Figure 3.8. Total number of foraging buzzes detected in logged and unlogged sites in fragmented stands, and control sites in unfragmented stands, in old aspen mixedwood forests in 1993 and 1994. In 1993, no sites had been logged. a) Total bats, b) *Myotis* spp. n=6 sites/treatment/year in fragmented stands, and 11 sites/treatment/year in unfragmented stands.

Table 3.2. Foraging effort (ratio of buzzes to passes) of total bats and *Myotis* spp. bats in logged and unlogged sites in fragmented stands, and control sites in unfragmented stands, in mature and old aspen mixedwood forests in 1993 and 1994.

Stand Age	Site Treatment	n	1993		1994	
			Total	*Myotis* spp.	Total	*Myotis* spp.
Mature	Logged	6	0.090	0.092	0.16	0.16
	Unlogged	6	0.24	0	0.054	0.070
	Unfragmented	11	0.054	0.11	0.061	0.14
Old	Logged	6	0.028	0	0.10	0.12
	Unlogged	6	0.025	0	0.012	0.077
	Unfragmented	11	0.11	0.11	0.060	0.069

bats were most active in the forest (Chapter 2). Although this difference was statistically significant in mature stands only, in old stands it was the absence of bats from centre and forest habitats that made statistical comparisons invalid.

Foraging habitat selection by bats is determined, at least on a gross scale, by their wing and echolocation call design (Aldridge and Rautenbach 1987, Fenton 1990). Within this framework, habitat selection depends on prey availability (de Jong and Ahlen 1991, Saunders and Barclay 1992, Brigham et al. 1992, Jones et al. in press) and may also be influenced by predation risk (Rydell 1989b, de Jong 1994) and inter- and intra-specific competition (Kunz 1973, de Jong 1994).

Edges may present the best combination of the above factors when compared to open clearcuts on the one hand, and dense aspen forest on the other. Edges are less cluttered than forests, making foraging and commuting easier. Several studies have suggested that insect abundance and density are higher along edges, particularly the lee edge, than in open habitat (Lewis 1970) or in the forest (Toda 1992). Bats often respond to localised accumulations of insects (e.g. Geggie and Fenton 1985, Furlonger et al. 1987, de Jong and Ahlen 1991), and may forage in more open habitat (than predicted by ecomorphology) such as edges if prey is more abundant there (Brigham et al. 1992, Saunders and Barclay 1992). Even when insect abundance is higher in open or forested areas, some bats choose to forage near the edge, perhaps to avoid predation (Estrada et al. 1993, de Jong 1994) or clutter (Kalcounis and Brigham 1995). Also, the edge may serve as a navigational corridor along which bats forage or commute to other habitats (Limpens and Kapteyn 1991). The vertical nature of forest edges also allows bats to forage at different heights (de Jong 1994) and thereby potentially reduce competition.

Although bats preferred edges in my study, it appears that this preference was weaker than that of bats in other systems (Leonard and Fenton 1983, Rydell 1986, de Jong 1994, Grindal 1995). Differences in the relative use of edge or forest habitat may

reflect variation in the clutter and prey distributions of the different forests, and the ecology of the bats in question. It may be that, unlike other systems, prey densities in the aspen forest do not differ greatly among edge, forest, and open habitats. When insects are evenly distributed among habitats, or are more abundant in the forest, some forests are preferred bat habitat (de Jong 1994, Kalcounis and Brigham 1995). The lack of a strong preference for the edge may also reflect the short time since fragmentation. Edges are often associated with a flush of vegetation in response to increased light following cutting (Chen and Franklin 1992), and thus an increase in herbivorous insects (Murcia 1995), but this effect may not be realized immediately. Moreover, bats may take some time to respond to new prey patches. The edges examined by Grindal (1995) were in clearcuts much older than those of my study. Edges of recently logged aspen mixedwood sites appear to be only slightly better foraging and commuting habitat than the forest.

The moderate activity in the centres of clearcuts in mature stands was surprising, given the numerous reports of bats avoiding open areas (e.g. Racey and Swift 1985, Krull et al. 1991), particularly for foraging (Rydell 1986, 1989b, de Jong 1994 in press). Moreover, in some areas bats prefer forests to surrounding open areas (Rydell 1989b, de Jong and Ahlen 1991, Kalcounis and Brigham 1995), including clear cuts (de Jong 1994). However, this pattern held only in mature forests; in old forests, the trend was toward greater activity in the forest than in the centre. Also, more foraging occurred in the forest in old stands than in mature stands. The contrast between the clutter of the forest, and the more open edge may be greater in mature stands, which have a greater density of trees and fewer gaps (Lee et al. 1995a), than in old stands. Therefore, bats may be more likely to use the logged sites in mature stands than those in old stands.

Difference in activity in sites after logging should reflect the combined effects of increased foraging habitat, and loss of roost trees. Activity in logged sites and unlogged sites did not generally differ significantly, given the high variation from site to site.

When compared to unlogged sites in fragmented stands, edges tended to have higher total and *Myotis* activity, and clearcut centres to have lower activity, however, again indicating that edges of logged sites may attract foraging and commuting activity. This increase may be due to greater prey abundance, or greater ease of movement and detection in the more open environment of the edge than the forest. The high rate of captures along edges in mature logged sites supports the contention that, particularly in this age of forest, open commuting lanes are important.

Foraging buzzes in logged sites increased slightly in old sites after logging; foraging effort (the ratio of buzzes to passes) increased slightly in both mature and old sites. *Myotis* spp., some of which often prefer edges (e.g. Fenton et al. 1980, Furlonger et al. 1987, Barclay 1991), in particular took advantage of the increase in this habitat. These results suggest that, given the activity in logged sites, relatively more foraging attempts occur. However, even after logging, the rates were lower than those detected over open water (Thomas 1988). Considering also the generally low activity (particularly in hour 2), I suggest that bats are primarily using the edges as commuting lanes to other feeding grounds such as bogs, ponds and older clearings in the forest, and are foraging opportunistically *en route*. Such behaviour has been observed in other bat species (Krull et al. 1991).

The absence of large increases in activity in logged sites may simply reflect the short time since logging (see above). The small sample size and great variability may also have precluded detecting a difference between edges or centres of logged sites and unlogged sites, as was the case in another study of the effects of fragmentation on mammals (Heske 1995). Thus, in several years' time, a further study may confirm statistically the general trend towards increased activity along edges of logged sites.

The general lack of significant increases in logged sites could also reflect the loss of roost trees, and consequent loss of bats, from the sites. Given the long distances that

can be traveled by bats to profitable feeding grounds (Racey and Swift 1985, Brigham 1991, de Jong and Ahlen 1991, de Jong 1994), this hypothesis at first seems unlikely; if logged sites were good foraging areas, bats would have been attracted from neighbouring forests, thereby compensating for the loss of bats in roost trees in the sites. However, in many cases (including this study, Chapter 2), bats in late pregnancy and lactation forage close to roost trees (de Jong in press), and thus may not be as likely to commute to forage in logged sites. Also, if roost trees are limiting in the aspen mixedwood forest, then a removal of roost trees may not only cause bats to be absent from the site, but may cause a decrease in the population.

The effects of the loss of roost trees are most likely to be seen by comparing unlogged sites in fragmented stands to those in unfragmented stands. In these sites, there is unlikely to be a flurry of activity resulting from changes in foraging opportunities; activity more likely represents bats commuting to roost trees and foraging in the forest. If roost trees are limiting, and the bat population is affected by their loss following fragmentation of the stand, then activity will diminish. This effect may be compounded by bats leaving the unlogged portions of the forest to forage along the edges of cut areas, thus decreasing activity in the forest itself. However, foraging opportunities in logged sites may not act as a stronger draw on bats from unlogged sites than do cutlines, ponds and bogs near unfragmented stands.

Total and *Myotis* activity levels in unlogged sites in fragmented stands did not change statistically following fragmentation, although there was a slight decrease in activity. Foraging rates of total bats decreased, particularly in mature stands. These trends may indicate a movement to logged sites for foraging. They may also represent a decrease in bat activity or perhaps abundance due to a loss of roost trees, even at this early date following fragmentation. Other animal species that depend on roost trees, particularly cavity trees, are less abundant in fragmented than unfragmented stands (birds:

Franzreb and Ohmart 1978, Keller and Anderson 1992; red squirrels *Sciurus vulgaris*: Wauters et al. 1994).

As in the other levels of comparison, the lack of statistical differences between stand treatments may result from the great variability in bat activity between sites, and/or the lack of time since fragmentation. Over time, logged sites may become more profitable as foraging grounds, and thus attract bats to fragmented areas. However, it is unlikely that foraging areas are in short supply in and near the aspen mixedwood forest, at least in old stands (Chapter 2). If roost trees are limiting, on the other hand, and thus the dominant factor in bat habitat selection, the trend towards a decrease in bat abundance in fragmented stands should become significant. Roosting environment is very important in ensuring that bats survive not only the summer, but the following winter (Thomas et al. 1990). Over time, it is likely that more roost trees will be lost from the system, for several reasons. As more forest is logged, the number of current roost trees and new recruits from which to draw will be reduced. Tree mortality and tree fall increases with decreasing patch size (Chen and Franklin 1992) and logging disrupts the replacement of snags (Cline et al. 1980) and cavity trees (Tidemann and Flavel 1987). In the aspen mixedwood, trees remain in the early decay stages preferred by bats (Chapter 2) for approximately 10 years (P. Lee, pers. comm.). In fragmented forests, many of these may not be replaced. In the next 10 years, this loss of roost trees may be felt, and a decrease in bat populations at the stand level may occur.

The use of fragmented forests by bats is a product of roosting and foraging opportunities. Currently, it appears that neither has been strongly affected by fragmentation, and thus bat activity and abundance remained largely unchanged. However, at this point in time, little of the aspen mixedwood forest has been logged. In the future, it is likely that localised foraging habitat (along edges) will become more profitable, while roosting habitat in fragmented forests becomes impoverished. This loss

of roosting habitat may be exacerbated by increased isolation of patches if old forests are not connected to other patches, as bats appear to avoid open areas. If roost trees are limiting in this system, and thus dominate habitat selection, it is likely that a decrease in bat abundance will occur.

CHAPTER 4

CONCLUSIONS AND RECOMMENDATIONS

Conclusions

In temperate regions, summer habitats must provide both roost sites and foraging grounds for insectivorous bats. Yet the selection of habitats based on both of these criteria has rarely been studied, and thus it is difficult to predict which factor, roost availability or foraging habitat, influences the habitat choices made by bats more heavily. In the aspen mixedwood forest, bat distributions in both unfragmented and fragmented stands of different ages reflect both roosting and (perhaps secondarily) foraging opportunities present in these habitats.

For roost sites, bats selected deep cavities in tall aspen trees of early decay classes and with low clutter; these trees likely provided consistently warm temperatures and adequate space for colonies, while offering protection from predators. Roosting activity depended on the availability of trees of sufficient size and decay class. Foraging activity appears to have been related to openness of habitats, and could also reflect insect abundances and predation risk. Both the availability of roost trees, and the openness of the habitat differed with stand age and treatment and bat activity and abundance varied accordingly. Activity decreased in areas with few roost trees and/or high levels of clutter.

In the aspen mixedwood, bats, in particular *Myotis* spp., were more abundant in old stands than in young and mature stands. Because both roost sites and foraging habitat were more abundant in old stands, it is difficult to determine which was the primary factor in attracting bats. Optimal combinations of roosting and foraging habitat for bats are probably more prevalent in old stands. However, it is possible that roost selection, particularly if roost trees are limiting, dominates selection of a general habitat.

By examining bat activity in fragmented stands, it is possible to begin to tease apart these two factors. Within a forest of a given age, fragmentation increases foraging

habitat by providing edges, which may offer greater prey abundance than the forest or the clearcut. Edges also are sheltered, yet less cluttered than the forest, particularly mature forest. However, fragmentation reduces the number of roost trees in the stands. In the short term, the increase in foraging activity along edges did not generally translate into an increase in bat abundance at the site or stand level, probably due to a loss of roost trees. In particular, it seems that fragmentation did little to enhance the foraging opportunities of the more open old stands, while it did remove valuable roost trees. In fact, there was a tendency for bat activity to be lower in stands following fragmentation, suggesting that the loss in terms of roost sites was greater than the gains in terms of foraging habitat.

The long term effects of fragmentation are likely to be more severe, as more of the aspen mixedwood forest is logged and put into 70 year rotation, and old forests and roost trees are lost. In general, there are three potential consequences of habitat fragmentation: isolation of remaining patches, reduction of patch size and loss of habitat (Andren 1994). These factors may affect bats to varying degrees. Given the large distances traveled by bats, isolation of patches is not likely to affect bat populations, provided there is a travel corridor along forested areas between habitat patches, as some bats avoid crossing open areas. However, the other two factors may come into play. In small patches, trees are subject to different temperature and humidity conditions (Williams-Linera 1990) and are more likely to die, due to the high proportion of edge (Chen and Franklin 1992). Thus, in small patches, bats are likely to be faced with fewer roost trees and trees with inappropriate conditions. The issue of habitat loss is complicated, because, as noted, foraging habitat may increase, especially if insect abundances increase in clear cuts. However, for bats, as for other species (birds: Keller and Anderson 1992, squirrels: Andren and Delin 1994), the major impact of fragmentation is likely to be that of absolute habitat loss, given that the amount of old forest, and the number of roost trees, is to be reduced under current logging practices, and bats are associated with roost trees in

old forests.

Selection of forest habitats by bats is a complex process, involving not only tradeoffs between roosting and foraging habitats, but also potentially tradeoffs between different factors influencing selection of each of these habitats in themselves. Forests of different types and ages provide excellent opportunities to study many aspects of roost site and foraging habitat selection, and the balance struck between the two in the choice of overall habitat. Experimental manipulations of the quality and availability of roosting and foraging sites, such as through the use of different logging regimes, can help us understand the relative importance of these factors. These studies will not only help us understand many important aspects of bat ecology, they will also help elucidate the many complex and intertwined factors that influence animals in general in their choice of habitats. Studies such as this one will also help managers plan resource exploitation in these habitats so that they minimize changes in the habitat features required to sustain viable populations.

Recommendations for further research

To better understand habitat selection by bats in aspen mixedwood forests, and thus perhaps mitigate the effects of fragmentation, some aspects of the ecology of forest-dwelling bats need to be clarified. First, a better understanding of the relative importance of the various factors involved in roost selection, and the number of trees used by individual bats is needed. Further studies thus should include a more thorough examination of the dimensions, characteristics and microclimate of roost cavities, predation and parasitism in roosts, and the reasons why bats switch roosts. To evaluate the suggestion that roost sites are limited, an attempt should be made to quantify the number of roost trees used by bats, and the number of trees available, using more stringent criteria for random wildlife trees than used in this study. Also, the consequences of roosting in low quality roosts should be assesed. More information on

the dynamics of aspen snags, especially in the early stages of decay, would be useful. Patch size may be of some importance, in that roost trees may be negatively affected by the climate of small patches; this possibility should be examined. A long term study of known trees in unfragmented stands may help determine population changes as fragmentation progresses in nearby areas, in that roost trees, and other apparently available trees, could be monitored for changes in occupancy.

Second, the importance of the aspen mixedwood forest, and old stands in particular, as foraging habitat needs to be clarified. Bats should be followed with radiotelemetry in fragmented and unfragmented stands to identify their foraging sites, and commuting distances. The relative influences of clutter and insect densities in determining foraging habitat should be assessed by concurrent insect trapping in forests, edges, centres of clearcuts, and near bogs and ponds. Again, seasonal shifts in foraging habitat should be monitored.

Suggestions for forest management

Before making suggestions for ways to minimize potentially adverse effects of forest harvesting on bats, it is important to recognize the limitations of my study. First, the study was conducted in a subset of stands in the aspen mixedwood forest, and may not fully represent conditions in other areas of this forest. Second, the data were only collected over a two year period and cannot fully address the long term consequences of forest harvesting. Third, there remain outstanding questions (discussed above) with respect to the importance of roosting and foraging sites in the aspen mixedwood forest. With these limitations in mind, I believe, based on the results of my study and those of other researchers, that the following issues should be considered by forest managers concerned with maintaining bat populations in the aspen mixedwood forest:

1) Old stands are important to bats, especially in terms of roost trees. Decreases in the

amount of old growth in aspen mixedwood forests may lead to declines in bat abundance.

2) Bats preferred to roost in large open cavities on average 10 m above the ground in dying or newly dead *Populus* spp. (especially aspen) of at least 20 m height and 35 cm DBH. Moreover, individual bats used several of these trees within a two to three week period, all within continuous forest. If roosting behaviours are not accomodated by retaining such trees within patches of old growth, bat populations may decline.

3) The results of this study and others indicate that bats avoid crossing open areas (e.g. 30 ha clear cuts). Connecting remnant patches of old growth by other forested areas that provide shelter for commuting bats may improve the suitability of such patches for bats.

4) Bats prefer edges (and avoid open areas) as foraging and commuting habitat. Therefore, in planning the size of cutblocks, the ratio of edge to open area should be considered. Cutblocks with relatively great amounts of edge are likely to provide better bat foraging habitat; large cutblocks appear to be low quality bat foraging habitat.

5) The loss of roost trees from logged stands may be lessened by leaving potential roost trees in cutblocks. Because of the chance of blowdown, and the short lifespan of early decay class trees, such efforts will be most successful if several steps are taken: a) leave smaller trees unharvested to grow to become roost trees; b) surround these trees with others to reduce blowdown and moderate climatic influences on the roost; c) leave roost trees close to the edge of the cutblock to minimize the distance bats must travel before reaching cover, and to reduce blowdown.

Although some of these measures are appropriate to species other than bats, some measures will be unfavourable to these species. Thus to manage the forest for the goal of maintaining biodiversity, compromises between the habitat requirements of these different groups need to be made.

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Appendix 1. Description of decay classes of trees.

Symbol	Decay class	Description
A	alive	All branches and top intact and alive. No major signs of decay.
PA	partly alive	Top or at least one major branch dying or dead. Rest of tree alive.
D	dead (6 classes):	
D1	well-developed canopy	Newly dead tree, retains all branches including smaller twigs and probably retains top. Shows little sign of rot. Bark is tight. Newly dead.
D2	moderate canopy	Tree retains all major branches, but not smaller twigs and probably, but not necessarily, retains top. Is losing bark.
D3	sparse canopy	Tree retains some major branches, but these may be reduced in length. May or may not retain top. Has lost much of bark or bark is loose.
D4	loose bark	Tree has no branches and may or may not retain top. Has lost almost all bark. Trunk is still quite firm.
D5	broken	Tree has lost top and bark (bark may be hanging loosely). Trunk is fairly rotten (both heart and sap rot) and may be unsteady.
D6	decomposed	Tree is greatly reduced in height. Trunk is rotten and unsteady; rotten wood can be pulled out with the fingers.

Appendix 2. Tree variables included in statistical analyses

Continuous Tree Variables (used in Discriminant Functions Analysis)

Diameter at Breast Height (DBH)

Tree Height

Distance to Canopy (from the top of the tree, to the tops of dominant surrounding
species)

Percent Bark (remaining on the tree)

Canopy Depth (the depth of leaves from the top of foliage to the bottom)

Percent Leaf (the percent of branches from the bottom of the tree canopy which
bear leaves)

Percent Bare Trunk (the percent of the trunk free of branches and leaves, i.e.
uncluttered)

Discrete Tree Variables (analysed with χ^2 or randomisation test)

Tree Species

Distance to Edge (divided into 5 categories of distance)

·Edge Area (divided into 5 categories)

Decay Class (see Appendix 1)

Top Condition (broken, intact or regenerated)

Bark Condition (tight, loose or flaking)

Canopy Class (categories based on number and size of remaining branches, from
all branches to none remaining)

Presence and Type of Rot

Appendix 3. Characteristics of individual trees and roosts used by *Myotis lucifugus* (*M.l.*) and *Lasionycteris noctivagans* (*L.n.*). For descriptions of decay classes, see Appendix 1, and for descriptions of variables analysed statistically, see Appendix 2. Trees are grouped by radiotagged bat, in order used (indicated by the number following the decimal point). Tree species: *P.t.* = *Populus tremuloides*, *P.b.* = *Populus balsamifera*, *Pop* = *Populus* spp.; Tops: b = broken, r = regrown, i = intact; Bark: t = tight, l = loose, f = flaking; Canopy class: wd = well-developed, m = moderate, s = sparse, n = none; Rot: hr = heart rot, sr = sapwood rot; Roost type: sc = scar, cr = crack, kh = knot hole, lb = loose bark, fc = feeding cavity, nc = nesting cavity. n/a: trees were in clear cut. Dashes (-): values could not be obtained.

Bat. Tree	Bat Sp.	Tree Sp.	DBH (cm)	Height (m)	Dist.Can (m)	Dist.Edge (m)	Edge.Area (m2)	Decay Class	Top	Bark
1.1	*M.l.*	*P.t.*	37.9	26	0	0	12	1	i	t/l
1.2	*M.l.*	*P.t.*	39.7	28	0	3.5	40	pa	i	t
2	*M.l.*	*P.t.*	41.9	22	0	0	100	1	i	t
3.1	*M.l.*	*P.b.*	44.7	14.5	0	0	200	3	b	t/l
3.2	*M.l.*	*P.b.*	49	20	-11	5	30	pa	r	t
3.3	*M.l.*	*P.t.*	44	25	-6	0	24	2	i	t/l
4.1	*M.l.*	*P.t.*	36.2	26.5	0	1	48	a	i	t
4.2	*M.l.*	*P.t.*	32	28	0	4	300	pa	i	t
5.1 5.1	*M.l.*	*Pop*	31.6	9	10	4	600	4	b	t/l
5.2	*M.l.*	*P.t.*	42.7	25.5	4	0	250	pa	i	t/l
5.3	*M.l.*	*P.t.*	39.1	31	0	4	60	a	i	t
6.1	*M.l.*	*P.t.*	37.8	27.5	-2	0	60	a	i	t
6.2	*M.l.*	*P.t.*	26.5	22	7	0	70	2	b	t
7 7	*M.l.*	*P.t.*	54	22.5	-5	0	8	2	i	t/l
8	*M.l.*	*P.t.*	52.5	7	n/a	-24.9	360	3	b	t/l
9	*M.l.*	*P.t.*	46.4	23	0	0	72	3	r	t/f
10.1	*L.n.*	*P.t.*	34.9	21.5	0	0	600	pa	r	t
10.2	*L.n.*	*P.t.*	36.4	25	0	2	375	a	i	t
11.1 11.1	*L.n.*	*P.t.*	39.4	22	0	10	40	1	i	t
11.2	*L.n.*	*P.t.*	59.5	16.5	n/a	-18.9	360	3	b	t
11.3	*L.n.*	*Pop*	63.8	11	7	0	48	6	b	t
12.1	*L.n.*	*P.t.*	44.8	27	0	5	80	a	i	t
12.2	*L.n.*	*P.t.*	52.2	38	0	6	15	a	i	t
13	*L.n.*	*P.t.*	27.5	24	-4	0	0	2	i	t/l
14.1	*L.n.*	*P.t.*	33	21	5	3	48	2	i	t/l
14.2	*L.n.*	*P.t.*	41.4	25	0	0	360	1	i	t
15	*L.n.*	*Pop*	35.1	12	3	0	360	5	b	t

(continued from preceeding page)

% Bark	Can. Cl.	Can.Dep (m)	% Leaf	% Bare	Rot	Roost #	Roost Type	Roost Ht. (m)	#bats (min.)	# Days (max.)
90	wd	0	0	80	hr	1	kh	17	53	-
95	wd	4	65	60	hr	1	cr (sc)	2	11	-
100	wd	0	0	60	n	1	fc	12	18	3
60	s	0	0	80	hr/sr	1	lb	10	4	3
100	wd	7	30	50	hr	1	fc	8	60	4
90	m	0	0	80	hr	1	-	-	-	1
90	wd	8	70	80	hr	1	cr (sc)	19	4	-
95	wd	8	75	70	n	1	kh	22	-	-
95	n	0	0	100	hr	1	sc (cr)	5.5	2	-
						2	lb	8	2	-
100	wd	7	20	70	n	1	sc (lb)	16	21	6
95	wd	17	80	65	n	1	kh (cr)	9.5	3	-
100	wd	10.5	90	60	hr	1	sc	9	3	-
100	m	0	0	30	n	1	kh	12	24	-
100	m	0	0	75	hr	1	fc (sc)	15.5	13	4
						2	sc	13.5	25	-
100	n	0	0	100	hr	1	cr	6	1	2
80	s	0	0	85	hr	1	nc	9	1	-
90	wd	2	50	90	n	1	nc	18.5	15	-
100	wd	17	100	30	n	1	kh	10	-	-
100	wd	0	0	60	n	1	kh	11	6	2
						2	fc	10	9	-
95	s	0	0	80	hr	1	-	-	-	2
100	n	0	0	100	hr/sr	1	kh	6.5	2	-
90	wd	15	90	55	n	1	kh	14	8	-
100	wd	10	60	40	hr	1	nc	18	4	-
90	m	0	0	65	n	1	cr	8	6	-
95	m	0	0	50	n	1	sc (cr)	3.5	24	-
100	wd	0	0	50	hr	1	kh (sc)	10	16	5
90	n	0	0	100	n	1	cr	11	1	-