

Habitat Selection by Bats in Fragmented and Unfragmented Aspen Mixedwood Stands of Different Ages

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ABSTRACT

To determine if bats prefer certain ages of aspen mixedwood forest for roosting and foraging, and to predict the impacts of logging on bats, we compared the relative abundances and foraging activities of bats in young, mature, and old stands in 1993 and 1994, using bat detectors. In 1994, we also assessed post-logging bat abundances in two of the mature and two of the old stands. We tracked radio-tagged *Myotis lucifugus* and *Lasionycteris noctivagans* to roost trees, which we measured and compared to a random sample of wildlife trees. Mean total activity of all bats was significantly greater in old than in young or mature stands. It also appeared greater in unfragmented than fragmented stands, but not significantly so. All 27 roost trees were in old forests. Bats preferred tall (mean: 22.0 m), newly dead *Populus* spp. with heart rot and low leaf cover (mean: 27%). Tree-roosting colonies were small (4–63 bats) and transient. Bats likely select trees large enough to house colonies and provide suitable temperatures, and these trees are only available in old stands. Roost preference likely explains observed activity patterns. To sustain bat populations in these forests, old stands must be retained and roost sites preserved by managing the forest at the stand level.

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). The availability of suitable roost sites is likely a primary factor in determining a bat's choice of a habitat (Kunz 1982). Bats choose roosts that provide protection from predators (Fenton et al. 1994), and suitable thermal environments, given metabolic and reproductive demands (Hamilton and Barclay 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; Saunders and Barclay 1992), and competition (Fenton 1990) or predation (Barclay 1989) are likely not as important.

Roost availability may influence foraging habitat, leading some bats to forage in poorer-quality habitat (Geggie and Fenton 1985), particularly if commuting is costly, but there is some evidence that bats travel long distances from roosts to foraging grounds (e.g., Brigham 1991; de Jong 1994). Unfortunately, few studies examine the relative influences of foraging and roosting requirements on habitat selection by bats or look at differences within habitats, such as forests, although forests potentially provide both roosting and foraging opportunities to bats.

Forests differ in structure and composition with age, location, and disturbance. In particular, 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; Newton 1994) and other shelter for bats, may differ. 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 influence bat habitat selection in that they create openings for foraging (e.g., Crome and Richards 1988), but also remove potential roost trees.

The effects of major disturbances, such as commercial harvesting, on bats are potentially two-fold. First, in the short term, forest fragmentation may create more open areas, particularly edge habitat, for foraging, but may cause a loss of roost trees. Second, forest harvest may truncate the age distribution of the forest by selectively removing older trees, and thus may represent a loss of preferred habitat, especially for roosting. The overall effects of fragmentation may reflect a combination of the predicted negative impacts on the availability of roost trees, and possible improvements to foraging habitat.

Historically, anthropogenic disturbances in the aspen mixedwood forest of northern Alberta were limited to roads and seismic exploration (Stelfox 1995). However, much of the aspen mixedwood forest in Alberta was recently 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). It is predicted that a change in age structure will occur in these forests due to logging (Stelfox 1995), and thus there is some concern for the future of bat populations.

The aims of our study were, therefore, (1) to determine whether bats are found primarily in certain ages of aspen mixedwood forest, and whether their use of the forest 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 that it is one of the first studies to examine bat habitat selection in forests on the basis of both foraging and roosting criteria, and to study bat abundance and behaviour in the same stands pre- and post-logging. By considering

these factors, we can gain a better understanding of the use that bats make of the boreal forest, and of general principles of bat habitat selection that we can use to recommend the preservation of forest features essential to bats.

METHODS AND MATERIALS

We conducted this study in the aspen mixedwood forest to the northwest and northeast of Lac La Biche, Alberta, between 54° and 55°N, and 111° and 113°W. This forest is dominated by *Populus tremuloides* (trembling aspen), and *Picea glauca* (white spruce) in upland mesic areas. The range of ages currently found in the forest is 0–150+ years, with few young stands (Stelfox 1995).

In the summers of 1993 and 1994, we worked in or near 12 pyrogenic stands selected by the Alberta Environmental Centre (AEC): four young (20–30 yrs), four mature (50–65 yrs), and four old (>120 yrs; Stelfox 1995). Each stand contained six randomly placed sites of 100 m radius. Thus, the design included four stands of six sites in each age, or 72 sites in total.

Effect of Stand Age
and Fragmentation
on Bat Abundance
and Foraging

In 1993, no harvesting had occurred in the area. 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 of 6 sites) were incorporated into approximately 30-ha clearcuts. The remaining mature and old stands, and all the young stands, were left intact as controls. “Logging” refers to the removal of trees at the *site* level, and “fragmentation” refers 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, we sampled one site per night, randomizing the site order, but ensuring that we monitored at least one site per stand in every four-week period. In 1994, we also ensured that we monitored one logged site each week. To evaluate bat diversity, abundance, and activity in each site, we identified and counted bat echolocation passes using QMC bat detectors during a two-hour period beginning 15 minutes after sunset. To differentiate between species groups, we set one detector at 25 kHz and one at 40 kHz. 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, we established a transect through the site centre, along which we monitored activity at stations for 20-minute periods. In unlogged sites, this transect crossed areas of differing canopy cover. In logged sites in 1994, we sampled three habitats: centre of the cutblock, edge of the cutblock, and forest surrounding the cutblock. We located the site centre (now in the clearcut) and identified the nearest edge, usually 100–250 m away. We then established a sampling position 50 m into the forest (perpendicular to the edge). We monitored bat activity at the centre of the cutblock for 20 minutes, while our assistant monitored activity in the forest. We then monitored at the edge for 20 minutes before returning to our original positions. This cycle continued for the two-hour monitoring period. Both 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. A given observer monitored the centre at some sites and the forest at others.

To determine foraging activity in the different ages and treatments, we also used the bat detectors. When bats attack insects, they increase the repetition rate of their echolocation pulses (Fenton and Bell 1979). We recorded the resultant “buzz” as we monitored passes.

Roost Selection

To obtain bats for radio-telemetry (and also enhance species identification), we caught bats in mist nets placed in gaps and cutlines within unlogged stands perpendicular to the edge of logged sites. In 1994, we radio-tracked 14 bats carrying 0.67-g radio-transmitters (Hamilton and Barclay 1994) to their roost trees. All bats weighed > 8 g, and were female. We preferentially tagged lactating and pregnant females.

We tracked each individual for one to two weeks, usually locating her roost tree every other day, and noting her general position each day. For measurements of residency time and distance between roosts, we only used trees for which we could ascertain arrival and departure date. We used the maximum number of days an individual could have resided in a given tree.

For roost trees, we recorded tree species, height, and diameter at breast height (DBH). We assigned trees to a decay class based on the condition of the top, number of branches, amount of bark, and presence of rot. We measured the percentage of leaf remaining, percentage of bare trunk, canopy class (based on the number and size of branches remaining), and canopy depth. We also recorded the roost type, entrance dimensions, and height on the tree.

At sunset, we observed a roost tree for 45–60 minutes, counted the number of bats that emerged, and noted bat behaviour at the tree. We recorded the direction, duration, and approximate distance (based on signal strength) of flight by the radio-tagged bat using radio-telemetry.

We also measured a random sample of wildlife trees, defined as live and dead trees with 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 1 × 2 cm in entrance size. To obtain this sample we used a T² method (Krebs 1989). In each site, we 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. We searched for a second tree in a 25-m radius hemisphere from the first tree. For each tree, we recorded the same characteristics as for roost trees.

STATISTICAL ANALYSES

Effect of Stand Age

Because activity in hour 1 and hour 2 in both years was not normally distributed, we proceeded in two stages for each year's data to assess differences in activity among stand ages. First, we considered only “occurrence”: whether bats were present (one or more passes detected) or absent in stands of different ages. For 1993 data, we 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. We then compared activity between different pairs of ages using a t-test on the least squares mean proportion of sites per stand. In 1994, due to lower sampling intensity, we used a chi-squared test to evaluate differences in occurrence among stand ages. Based on the 1993 results (see below), we first compared young stands to mature stands. If there was no significant difference, we pooled data from young and mature stands and compared the pooled data to data from old stands. In both years, we analyzed each hour separately and repeated the procedure on data for *Myotis* and *L. noctivagans*.

In the second stage of analysis, for each year we contrasted total bat activity among ages in hours 1 and 2 for sites in which bats were present. We conducted ANCOVA on log-transformed data with age as a main effect, stand nested within age, and ambient temperature and date as covariates. We specified a random term for stand. We conducted pairwise t-tests to determine which ages differed in mean activity using $\alpha = 0.017$ as the level of significance (Zar 1984). There were insufficient data to conduct this test for *Myotis* or *L. noctivagans*.

To determine if foraging activity differed among ages, we used a chi-squared test to compare the observed number of feeding buzzes to the expected number (based on sampling intensity) among ages. We conducted this test for total *Myotis* and *L. noctivagans* buzzes in each year.

Roost Selection

There were no clear differences between the species' selection of any tree characteristic (Table 1; ANOVA: $0.003 < F < 0.41$, $0.53 < p < 0.95$), and thus values for the two species were pooled in subsequent analyses. Because all roost trees were found in old stands, we compared continuous variables of roost trees and random wildlife trees in old stands using a stepwise discriminant functions analysis (DFA). For this analysis, we used only three random trees per site. We then conducted a canonical discriminant functions analysis on the same data with the significant variables.

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

Effect of Fragmentation

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

The effect of fragmentation on activity in fragmented stands should be viewed in the context of the general increase in bat activity from 1993 to 1994 (see Results). To control for year-to-year differences, we compared the magnitude and direction of the change in number of captures or passes, from 1993 to 1994, between treatments. In other words, fragmentation affected bat activity only if the amount of the change in treated sites from 1993 to 1994 differed from that of control sites.

We compared bats' use of unlogged sites in fragmented stands to that of sites in unfragmented stands with two-way ANOVA, with year and

TABLE 1

Tree and roost characteristics	<i>Myotis lucifugus</i> n = 16 trees	<i>Lasionycteris noctivagans</i> n = 11 trees	F	P
<i>Tree</i>				
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
Percent bare trunk	71.6 ± 4.44	65.5 ± 7.21	0.11	0.74
Tree distance (m) ¹	1050 ± 251.7 (n = 9)	280 ± 66.3 (n = 5)	—	—
<i>Roost</i>				
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)	—	—
No. of bats	15.3 ± 4.55 (n = 16)	9.10 ± 2.27 (n = 10)	—	0.83 ²

¹ Tree distance is the horizontal distance between consecutive roost trees.

² Mann-Whitney test.

— Not calculated.

stand treatment as main effects, and site as a nested effect. The interaction indicated whether stand treatment affected bat activity. In some cases we used Mann-Whitney tests to compare the effect of fragmentation on the difference in activity between years.

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. We used $\alpha = 0.05$ as the level of significance unless otherwise stated.

RESULTS

We confirmed the presence in all stand ages of *L. cinereus* (hoary bat), *L. noctivagans*, *E. fuscus* (big brown bat), *Myotis lucifugus*, and *Myotis septentrionalis* (northern long-eared bat). Most (70–75%) of the echolocation activity was from *Myotis* spp., followed by *L. noctivagans*, *E. fuscus*, and *L. cinereus*.

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, although the difference was not significant (ANOVA: $F = 2.21$, $df = 1,10$, $p > 0.1$). Total activity in mature and young stands remained low over both summers.

Effect of Stand Age

In both years, relative total abundance of bats was greater in old stands than in mature or young stands in hour 1; in hour 2, there were no significant differences in any case. In 1993, the occurrence of total bats was

significantly higher in old stands (82%) than in young stands (39%; overall $F = 6.64$; $df = 2,9$; $p < 0.05$, $t = 3.3$; $df = 9$; $p < 0.01$; Figure 1), but did not differ significantly from that of mature stands (68%; $t = 1.36$; $df = 9$; $p > 0.2$). In 1994, the difference in occurrence between young and mature stands was not significant (Yates' $\chi^2 = 0.01$; $df = 1$; $p > 0.9$), but it was significantly higher in old sites (11 of 12 sites, 92%) than in young and mature sites combined (17 of 32 sites, 53%; Yates' $\chi^2 = 4.1$; $df = 1$; $p < 0.05$; Figure 2).

The pattern of occurrence of *Myotis* spp. in different stand ages was similar to that of total bats (Figures 1 and 2). In 1993, the occurrence of *Myotis* was significantly greater in old stands (75%) than in young stands (21%; $t = 3.3$; $df = 9$; $p < 0.01$; overall $F = 6.0$; $df = 2,9$; $p < 0.025$) in hour 1. In 1994, the occurrence of *Myotis* in old sites (10 of 12, 83%) was significantly greater than in the other ages combined (5 of 32 sites, 16%; Yates' $\chi^2 = 14.92$; $df = 1$; $p < 0.001$). The occurrence of *L. noctivagans* was low in all stand ages in both years (Figures 1 and 2). There were no significant differences in either year, although occurrence appeared greatest in old stands in 1994.

In 1993, when bats were present, old stands appeared to have greater total bat activity, but differences were not significant (Figure 3). 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 per hour (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.

Foraging activity was generally low in most sites, although it was high in a few sites near large gaps. We heard a total of 127 buzzes in 129 hours (0.98 buzzes per hour) in 1993, and 74 buzzes in 88 hours (0.84 buzzes per hour) in 1994. In both years, total foraging activity was greater than expected in old stands and lower than expected in young and mature stands combined (1993: $\chi^2 = 53.5$; $df = 1$; $p < 0.001$; 1994: $\chi^2 = 167.0$; $df = 1$; $p < 0.001$; Figure 4). *Myotis* foraging activity was also significantly greater in old stands in both years (1993: $\chi^2 = 69.2$; $df = 2$; $p < 0.001$; 1994: $\chi^2 = 147.8$; $df = 2$; $p < 0.001$), as was *L. noctivagans* foraging activity (1993: $\chi^2 = 7.91$; $df = 1$; $p < 0.005$; 1994: $\chi^2 = 24.0$; $df = 1$; $p < 0.001$).

Roost Selection

In 1994, we observed 15 trees used by 10 female (one pregnant, four lactating, three non-reproductive, one unknown) *M. lucifugus*, and 11 trees used by six female *L. noctivagans* (two pregnant, one lactating, two post-lactating, and one juvenile). A total of 26 roost trees, all *Populus* spp., and all in old stands, were measured. Mean roost tree height and DBH were 22.3 m and 41.0 cm for *M. lucifugus* and 22.1 m and 42.5 cm for *L. noctivagans*.

Myotis lucifugus and *L. noctivagans* both roosted predominantly (19 of 28 roosts) in deep cavities that appeared to have originated as cracks, scars, or knot holes; these roosts held the largest colonies (6–60 bats; 15 roosts). Two *M. lucifugus* roosts (of two and four bats) were under loose bark, both in trees of decay class D3 and D4. Mean, median, and maximum colony sizes of *M. lucifugus* were 15.3, 7.5, and 60 bats, respectively, and of *L. noctivagans* were 9.1, 7.0, and 24 bats, respectively (Table 1). Mean roost height was 11.4 m for *M. lucifugus* and 11.0 m for *L. noctivagans*.

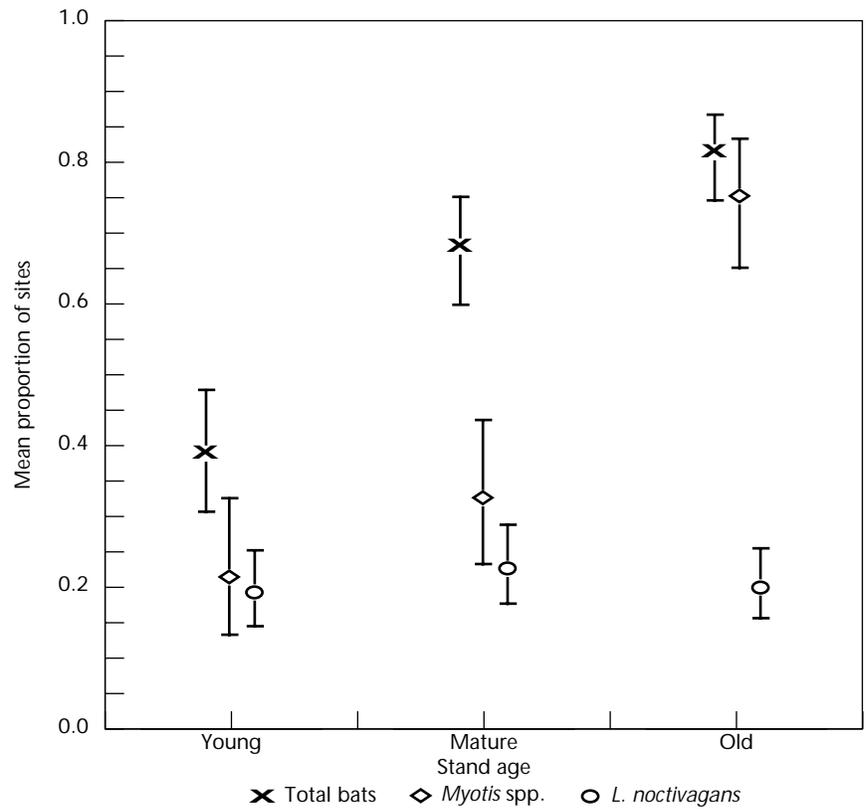


FIGURE 1 The mean (\pm S.E.) proportion of sites in aspen mixedwood stands of different ages in which at least one bat was detected in hour 1, 1993. Means and S.E.s were calculated from log-transformed data, and thus S.E.s are asymmetrical. $n = 4$ stands/age, and from 4–6 sites/stand.

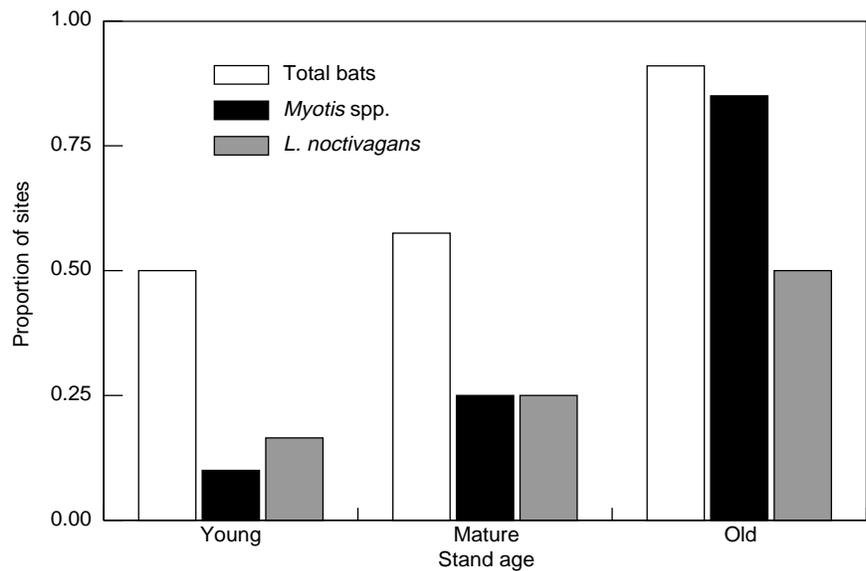


FIGURE 2 The proportion of sites in aspen mixedwood stands of different ages in which at least one bat was detected in hour 1, 1994. Young: $n = 20$, Mature: $n = 12$, Old: $n = 12$ sites.

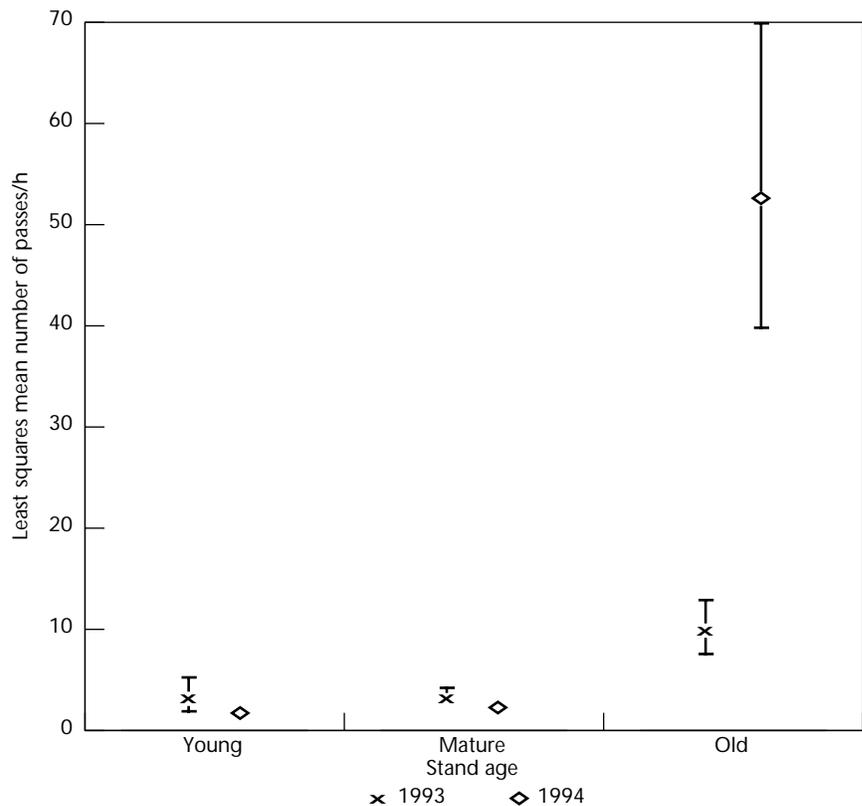


FIGURE 3 Least squares mean number (\pm S.E.) of total bat passes per hour detected in aspen mixedwood stands of different ages in 1993 and 1994. Means are based only on sites in which at least one bat was detected, and calculated from log-transformed data, thus S.E.s are asymmetrical. 1993 Young: $n = 7$, Mature: $n = 16$, Old: $n = 21$; 1994 Young: $n = 10$, Mature: $n = 7$, Old: $n = 11$.

Colonies were transient (mean residency time: 3.3 ± 1.6 days). Bats did not remain together, as individuals from a colony moved to different trees. Bats often moved several hundred metres between roost trees (mean distance: 775 ± 710 m, $n = 14$).

Tree height and percentage of leaf significantly discriminated between roost and random trees in old stands; the former explained 11.9% and the latter 22.2% of the variation between the two groups. Roost trees tended to be taller and of a lower percentage of 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%. Roost trees were also taller, and had a lower percentage of leaf than random trees in young and mature stands (Table 2, Figure 5). Random trees in these ages were also of lower DBH, were further below the canopy, and tended to be more cluttered.

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 6). Bats preferred trees of decay classes D1 and D2 ($G = 12.6$, $p < 0.025$, Figure 7), and of moderate canopy class ($\chi^2 = 6.40$; $df = 2$; $p < 0.05$), given their low abundance among old random trees, and indeed, wildlife trees in all ages.

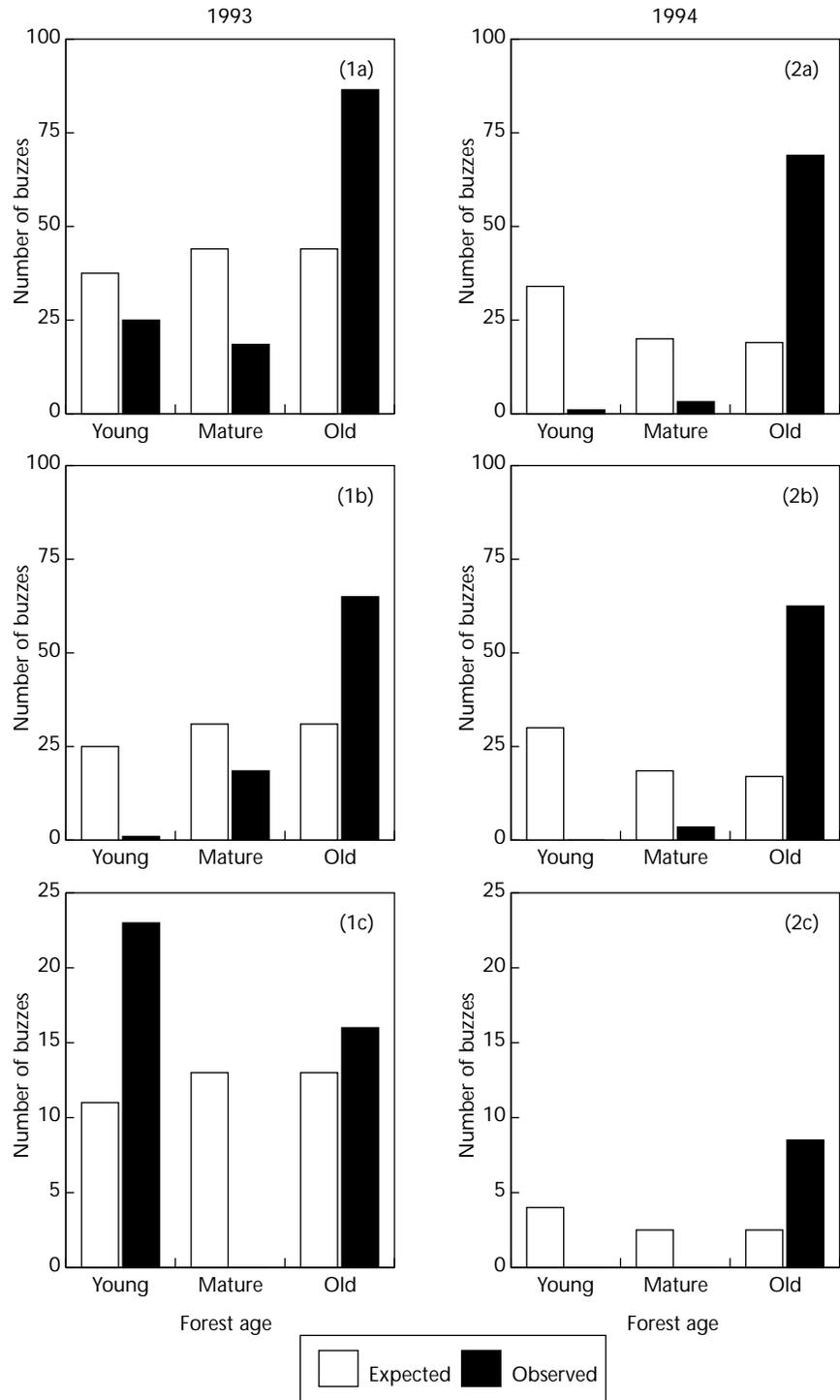


FIGURE 4 Comparison of observed to expected (based on sampling effort) number of feeding buzzes for different species groups in young, mature, and old aspen mixedwood stands. In each year: (a) total, (b) *Myotis* spp., (c) *L. noctivagans*.

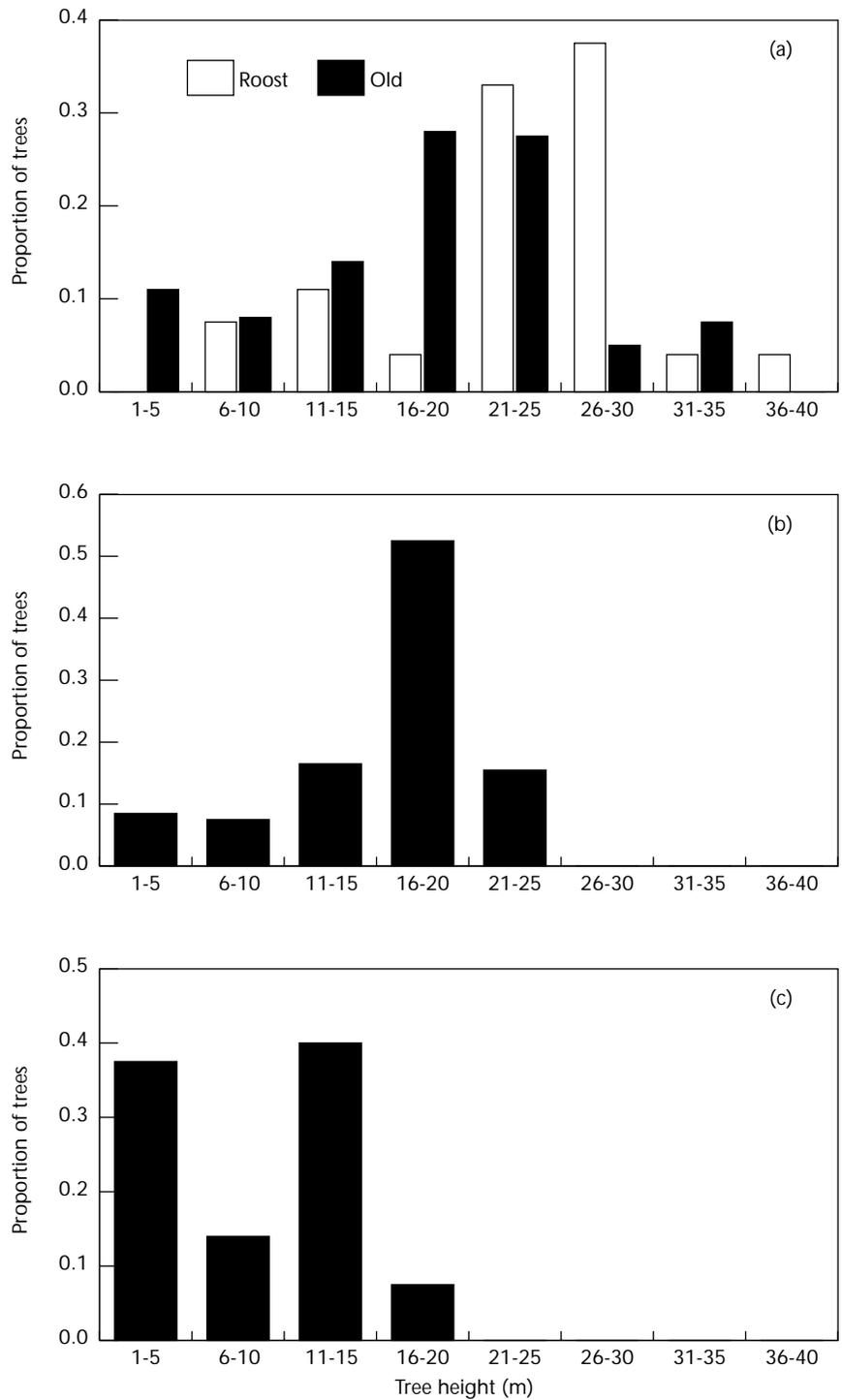


FIGURE 5 *Relative proportions of trees of different heights in samples of (a) roost trees, and random trees in old, (b) mature, and (c) young aspen mixedwood stands. Roost: $n = 27$, Old: $n = 64$, Mature: $n = 127$, Young: $n = 112$. For old sites, I included only the first random tree at each bearing; for young and mature sites, I included both trees.*

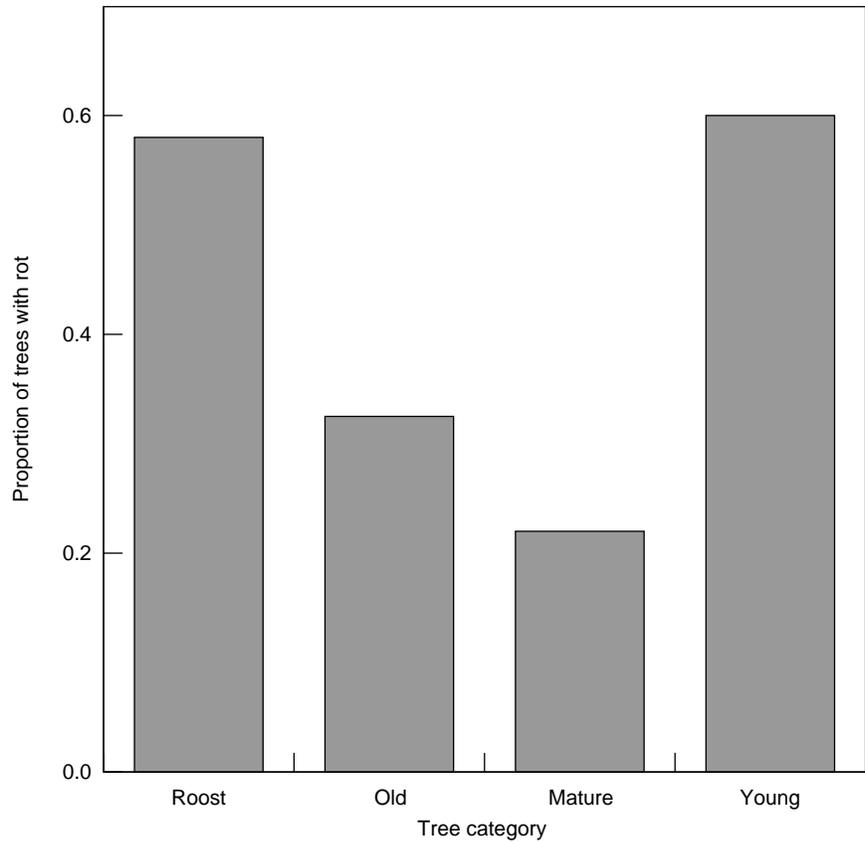


FIGURE 6 *Relative proportions of trees with rots in samples of (a) roost trees and random trees from old, (b) mature, and (c) young aspen mixedwood stands. Roost: n = 27, Old: n = 127, Mature: n = 127, Young: n = 109. In all ages, I included both trees sampled at each bearing in each site.*

Effect of Fragmentation

In logged sites, bats appeared to prefer the edge habitat in both mature (Figure 9) and old stands, followed by centre, then forest. We could not draw any statistical conclusions for old stands; given the low numbers of bats detected in the forest and the centre, activity was not normally distributed within these classes. In mature stands, activity among habitats differed significantly ($F = 5.07$; $df = 2,14$; $p < 0.025$); bats were more active along the edge than in the forest.

Activity following fragmentation was either 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 (Figure 10a). Total activity in mature stands showed a different pattern from that of other species and ages, in that it decreased slightly in both control and fragmented stands (Figure 10b).

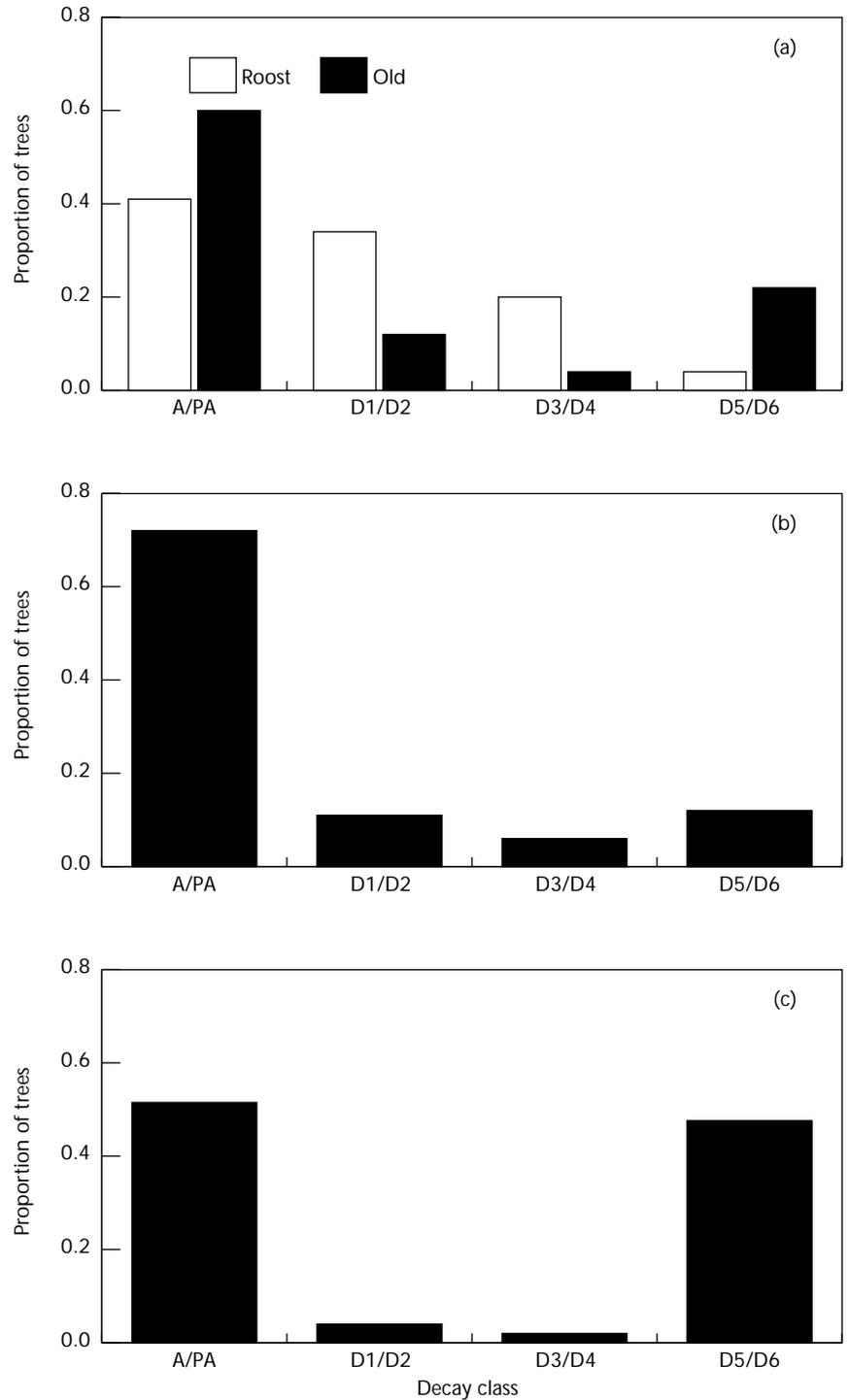


FIGURE 7 Relative proportions of trees in different decay classes in samples of (a) roost trees, and random trees from old, (b) mature, and (c) young aspen mixedwood stands. Roost: $n = 27$, Old: $n = 127$, Mature: $n = 127$, Young: $n = 112$. In all ages, I included both trees sampled at each bearing in each site.

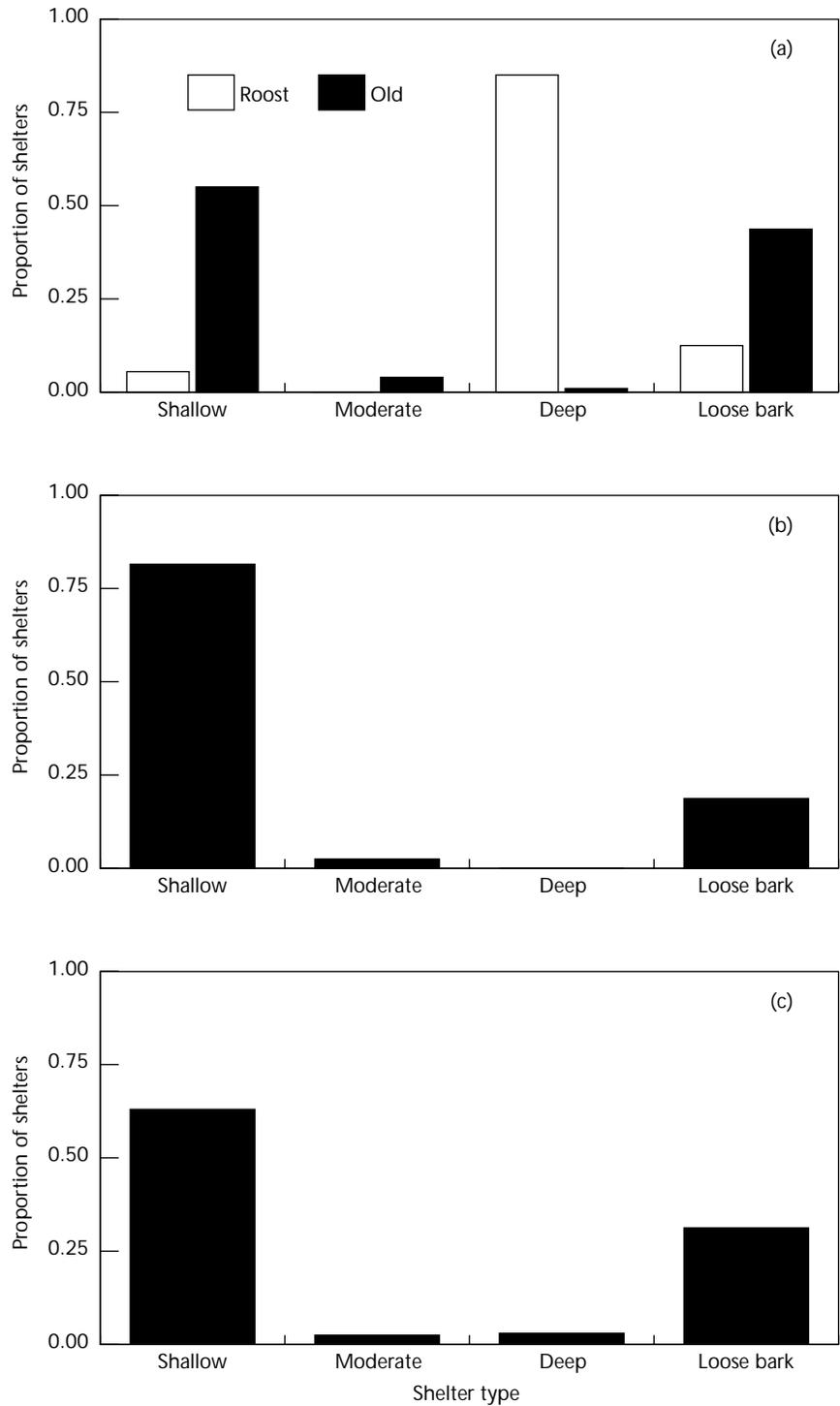


FIGURE 8 *Relative proportions of different types of shelter (based on depth and type) found in (a) roost trees, and random trees in old, (b) mature, and (c) young stands. Cavities and cracks: shallow (1–10 cm deep), moderate (11–20 cm deep), deep (>20 cm). Loose bark: 2–50 cm deep. Roost: n = 25, Old: n = 284, Mature: n = 219, Young: n = 179 shelters.*

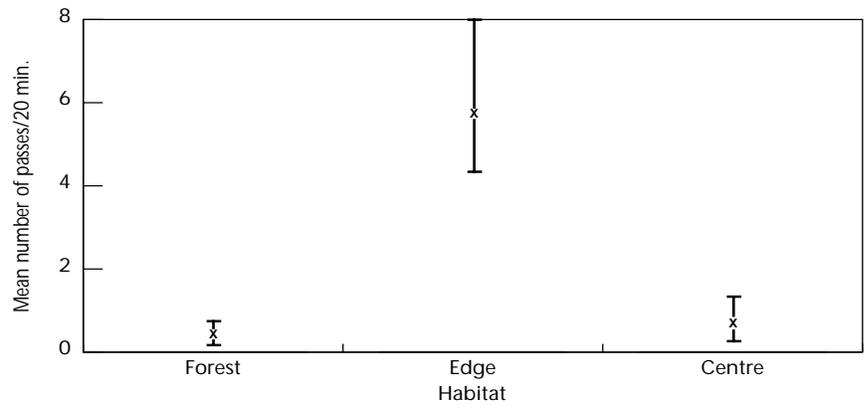


FIGURE 9 Mean (\pm S.E.) number of passes/20 minutes detected in different habitats of logged sites in mature aspen mixedwood stands, 1994. Means and S.E.s were calculated from inverse-transformed data, thus S.E.s are asymmetrical. $n = 6$ sites/habitat.

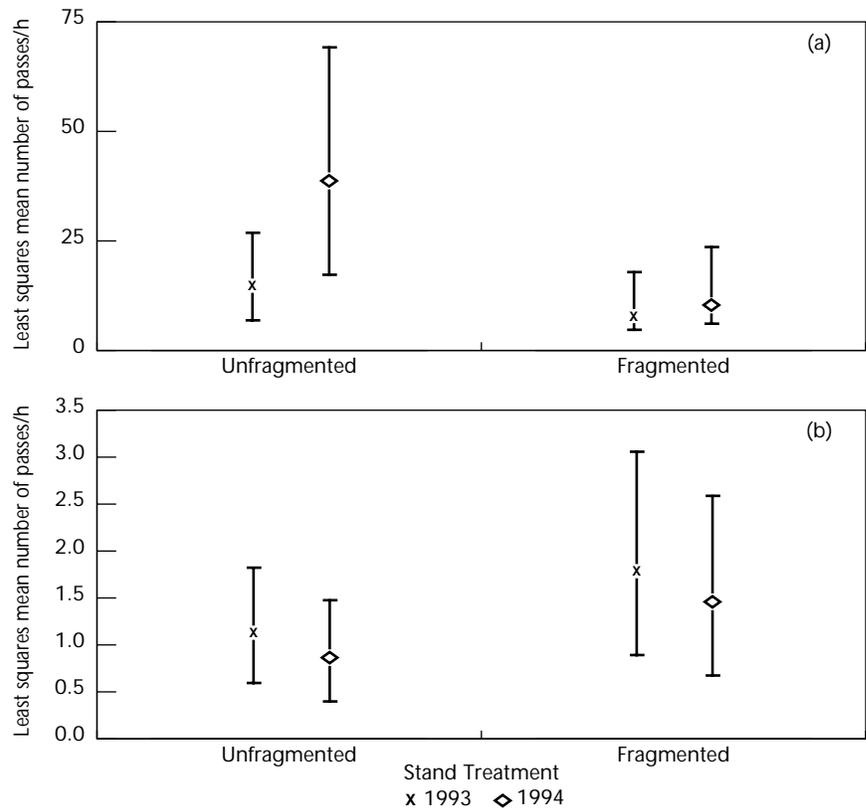


FIGURE 10 Least Squares Mean (\pm S.E.) number of total passes per hour detected in unfragmented and fragmented (a) old and (b) mature aspen mixedwood stands in hour 1 in 1993 and 1994. In 1993, fragmented stands had not yet been logged. Means and S.E.s were calculated from log-transformed values, and 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.

Effect of Stand Age

Bat occurrence in both years, and activity in 1994, were highest in old stands, indicating that bats prefer this forest age. In 1994, occurrence was higher in old stands than in both the other ages, while in 1993 it was greater in old stands than in young, but not mature stands. In both years, *Myotis* occurrence in old stands was greater than that in mature stands. Lower 1993 temperatures may have depressed bat abundance and activity by reducing reproductive success (Fenton et al. 1980; Lewis 1993), the number of bats in flight (Grinevitch et al. 1995), and duration of flight (Barclay 1985; Rydell 1989a), diminishing sample size and making it more difficult to detect differences in abundance among stand ages.

Old forests may contain habitat features required by bats, particularly *Myotis* spp., that are not present in any other ages. 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 bats (Barclay 1985, 1991; Furlonger et al. 1987; this study). 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.

The higher numbers of total and *Myotis* passes and buzzes indicate that many bats are attracted to old stands for foraging. Many *Myotis* spp., including *M. lucifugus*, prefer to forage in open areas (Barclay 1991; Saunders and Barclay 1992), particularly if prey abundance is greater there (Brigham et al. 1992). In particular, *M. lucifugus* forages along the edge of vegetation (Furlonger et al. 1987; Kalcounis and Brigham 1995), and thus may use gaps present in old stands.

Availability of foraging opportunities in old stands may not be the driving factor in the selection of this stand age by bats, given the presence of other foraging sites, such as lakes, in our study area. Some bats, especially *M. lucifugus* (Barclay 1991; Saunders and Barclay 1992) often prefer water bodies to other habitats, and will travel several kilometres to them from roosts (Brigham 1991; de Jong 1994). Alternatively, bats may not leave the forest, but forage over bogs, puddles, and small clearings in the forest. Regardless, the low number of buzzes detected suggests that the stands themselves may not be of great importance for foraging. At this point, we cannot completely elucidate the role of foraging behaviour in attracting bats to old stands, but roost-site selection may be more important.

We found bat roost trees only in old stands. Comparison of characteristics of roost and random trees in old stands showed that female bats selected deep cavities in tall aspen trees that were of a low percentage of leaf, early decay class, and moderate canopy class, and with rot. In young and mature stands, few wildlife trees matched these criteria. In particular, in young and mature stands, most wildlife trees were short and small, and of inappropriate decay class. 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.

We focused on roosts used by female bats because selection of a warm (McNab 1982), protected, maternity roost environment is critical to bats'

reproductive success. Bats selected trees and roosts which reflected these factors: roosts in tall, large trees with rotten centres that can be accessed through deep cavities are likely warm, spacious, and protected from predators. For example, roosts in large trees may have thicker walls, and thus extra insulation, than those of small DBH, resulting in more stable roost temperatures (Sluter et al. 1973). Trees of early decay classes also 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).

Deep cavities, high in trees, also provide thermal and social benefits and may offer protection from predators. Loose bark pieces could not hold the numbers of bats found in some cavities. Cavity roosts may have more stable and/or warmer temperatures, and be more humid (McComb and Noble 1981) than loose bark, which is thin in aspen.

Bats switched roost trees often, despite the potential costs in terms of lost social interactions and familiarity with an area (Lewis 1995). Roost switching may be important for maintaining healthy populations, as it may enable bats to reduce predation (Fenton et al. 1994) and parasitism (Lewis 1993), and use different microclimates (Lewis 1995). 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 we 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. Given their apparent scarcity, roost trees may drive habitat selection in aspen mixed-wood forests. Another explanation is that bats select old stands as the best combination of both roosting and foraging opportunities. However, the fact that differences in foraging opportunities (e.g. presence of gaps) among stand ages were less striking than differences in roosting opportunities, supports the first idea.

Effect of
Fragmentation

Any changes in bat abundance in forests following fragmentation 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.

We predicted that fragmentation would increase foraging and commuting habitat through the creation of edges. Within logged sites, bats generally preferred the edge of cutblocks to the forest or the centre of a clearcut. For foraging, edges may represent the best combination of several factors when compared to open clearcuts or dense aspen forest. Edges are less cluttered than forests, making foraging and commuting easier and serving as a navigational corridor (Limpens and Kapteyn 1991). Also,

insect abundance and density may be higher along edges, particularly the lee edge, than in open habitat (Lewis 1970) or in the forest (Toda 1992). Even when insect abundance is higher in open areas, some bats choose to forage near the edge, perhaps to avoid predation (Estrada et al. 1993; de Jong 1994).

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.

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. These trends may 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. With time, logged sites may become more profitable as foraging grounds, as vegetation and insects flourish, and bats are attracted 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. If roost trees are limiting, by contrast, and thus the dominant factor in bat habitat selection, the trend towards a decrease in bat abundance in fragmented stands may become significant. 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). If trees currently in early decay stages are not replaced in the next 10 years, a loss of roost trees 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. It appears that neither was strongly affected by fragmentation in the short term, and thus bat activity and abundance remained statistically unchanged. However, little of the aspen mixedwood forest has been logged to date. In the future, it is likely that localized 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 (de Jong 1994). If roost trees are limiting in this system, and thus dominate habitat selection, it is likely that a decrease in bat abundance will occur.

Before suggesting ways to accommodate bats in managed forests, it is important to recognize the limitations of our study. First, it 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 with respect to the importance of roosting and foraging sites in the aspen mixedwood forest. With these limitations in mind, we propose the following issues for consideration:

1. Old stands are important to bats, especially in terms of roost trees. Decreased amounts of old growth in aspen mixedwood forests may lead to declines in bat abundance. Connecting remnant patches of old growth via other forested areas that provide shelter for commuting bats may improve the suitability of such patches for bats.
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. If roosting behaviours are not accommodated by retaining such trees within patches of old growth, bat populations may decline.
3. Bats preferred edges (and avoided open areas) as foraging and commuting habitat. 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.

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