Journal of Applied Ecology 2003
40, 646–657

Foraging by bats in cleared, thinned and unharvested boreal forest

KRISTA J. PATRIQUIN and ROBERT M. R. BARCLAY
Department of Biological Sciences, University of Calgary, Calgary, Alberta, Canada T2N 1N4

Summary

1. Modern silvicultural methods employ various styles of selective harvesting in addition to traditional clear-cutting. This can create a mosaic of patches with different tree densities that may influence habitat use by foraging bats. Use of forest patches may also vary among bat species due to variation in their manoeuvrability. Apart from studies investigating use of clear-cuts, few have tested for differences in use of forest patches by bats, or for differences among bat species.
2. We investigated the influence of various harvesting regimes, which created forest patches of different tree densities, on habitat selection by foraging bats in the boreal mixed-wood forest of Alberta, Canada. We also tested for variation in habitat selection among species related to differences in body size and wing morphology.
3. Over two summers we assessed habitat use by bats using ultrasonic detectors to count the echolocation passes of foraging bats. We measured activity in three forest types and four tree densities, ranging from intact (unharvested) forests to clear-cuts.
4. Smaller, more manoeuvrable, species (*Myotis* spp.) were less affected by tree density than the larger, less manoeuvrable, *Lasionycteris noctivagans*. Two *Myotis* spp. differed in their habitat use. *Myotis lucifugus*, an aerial insectivore, preferred to forage along the edge of clear-cuts, while *M. septentrionalis*, a species that gleans prey from surfaces, did not forage in clear-cuts but preferred intact forest.
5. The largest species in our study, *L. noctivagans*, preferred clear-cuts and avoided intact patches. There were therefore differences in habitat selection by foraging bats among the species in our study area, and these were correlated with size and wing morphology.
6. *Synthesis and applications*. Our results suggest that, in the short term, thinning has minimal effect on habitat use by bats. They also indicate that silvicultural methods have different immediate effects on different species of bats that may be obscured if the community is studied as a single entity. Management for forest-dwelling bats must take such species-specific effects into consideration. Harvesting that creates a mosaic of patches with different tree densities is likely to satisfy the requirements of more species than a system with less diverse harvesting styles.

Key-words: Chiroptera, clear-cut, forestry, habitat use, logging, silviculture, thinning

Journal of Applied Ecology (2003) **40**, 646–657

Introduction

Historically fire, floods and insect outbreaks created a mosaic of habitat patches in forests (Hansson 1992). In many cases, anthropogenic disturbances such as logging and agriculture now contribute to forest patchiness. Logging was traditionally achieved through clear-cutting (Stelfox 1995) but in an effort to mitigate the effects, as well as to maximize timber yield, new harvesting regimes have been implemented (Walker *et al.* 1996), such as selective logging. Selective logging includes group selection cutting, dimension felling, single tree selective cutting and thinning. Thinning may be performed to: (i) maximize growth of remaining trees; (ii) emulate the structure of old-growth forests; (iii) emulate fire or other natural disturbances (Humes, Hayes & Collopy 1999). Practising different harvest regimes (i.e. clear-cutting and thinning) together in a

Correspondence: Robert Barclay, Department of Biological Sciences, University of Calgary, Calgary, AB, Canada T2N 1 N4 (fax +403 289 9311; e-mail barclay@ucalgary.ca).

© 2003 British Ecological Society

given area results in a mosaic of forest patches, which may create patchily distributed resources for forest-dwelling animals.

Habitat selection by bats may be influenced by the patchiness created by logging. The majority of more than 1000 species of bats are insectivorous, including all 18 species found in Canada. Many bats are forest-dwelling (van Zyll de Jong 1985) and rely on forests for both food and shelter. Insectivorous bats also perform important ecological roles as the primary predators of nocturnal, flying insects (Altringham 1996). The conservation status of species in Canada is based in part on the significance of potential threats to habitat (COSEWIC 2001), and a considerable amount of Canada's forests is allocated to harvesting, oil exploration and agriculture. Forest management thus has the potential to affect significantly populations of forest-dwelling bats and the ecological roles they play.

Patchiness created by harvesting may influence habitat use by foraging bats directly, due to effects on flight, and indirectly, via effects on prey and roost abundance. Flying bats must contend with physical clutter (i.e. vegetation; Fenton 1990; Brigham *et al*. 1997) that reduces flight efficiency (Norberg 1981; Jones & Rayner 1991). Furthermore, the use of echolocation to detect obstacles and potential prey means that higher vegetation density results in greater acoustical clutter (Mackey & Barclay 1989; Fenton 1990), perhaps further reducing foraging efficiency. None the less, some bats avoid open areas, perhaps to avoid predators or high winds that interfere with flight or prey capture (Verboom & Spoelstra 1999).

Prey abundance in forests can also be influenced by vegetation density and harvesting regimes. In some cases, insect abundance in harvested areas is similar to that observed prior to harvest (Grindal & Brigham 1998), while in other forests insects are more abundant in areas with greater tree density (e.g. intact forest) than in harvested areas (Grindal 1996; Burford, Lacki & Covell 1999). Bats may thus face a trade-off between food-poor patches with minimal physical and acoustical clutter vs. richer but more cluttered habitats. Different bat species resolve this trade-off differently. Larger species must fly quickly, thus compromising their manoeuvrability, whereas smaller species can fly more slowly and manoeuvre more easily (Norberg & Rayner 1987). Consequently, larger species are generally limited to more open habitat whereas more manoeuvrable species can exploit richer food sources in more cluttered habitat (Aldridge & Rautenbach 1987; Crome & Richards 1988; Fenton 1990; Kalcounis & Brigham 1995).

At the population level, the impact of disturbances such as logging depends on the disturbance history to which species have been exposed, the behaviour of the species and their life histories (Andrén 1994; Kavanagh & Bamkin 1995; Schieck *et al*. 1995; Robinson & Robinson 1999). Animals, such as bats, that are long lived and have low fecundity (Tuttle & Stevenson 1982), may be especially sensitive to anthropogenic disturbances due to changes in availability of food and shelter (Bright & Morris 1996; Law 1996; Parker, Cook & Lewis 1996), although the mobility of bats may allow them to avoid local disturbances by exploiting suitable habitat patches at a larger spatial scale.

Although the influence of logging on habitat use by foraging bats has recently received considerable attention (Barclay & Brigham 1996), few studies have addressed this influence experimentally. Furthermore, studies yield conflicting results (Crampton & Barclay 1996; Grindal 1996; Hayes & Adams 1996; Parker, Cook & Lewis 1996), possibly because they address entire bat communities or species groups rather than individual species. Differences in habitat use may become apparent only when individual species are investigated (Law, Anderson & Chidel 1999; Law & Anderson 2000; Pavey & Burwell 2000; Menzel *et al*. 2002).

Many studies have compared habitat use by bats in clear-cuts or gaps and adjacent intact forest, as well as between habitat edges and the centre of clear-cuts or gaps (Limpens & Kapteyn 1991; Walsh & Harris 1996; Verboom & Spoelstra 1999; Menzel *et al*. 2002). Few studies have investigated the response of bats to thinned forests (but see Perdue & Steventon 1996), despite the increased use of this harvesting practice (Humes, Hayes & Collopy 1999). As the structure of a harvested forest changes over time, it is important to investigate habitat use by bats over a range of time periods. Humes, Hayes & Collopy (1999) tested the effect of thinning on bat communities several years after harvest in regenerating forests previously logged or burned in the early to mid-1900s. Overall bat activity was greater in old-growth and thinned regenerating forest than in unthinned regenerating forest, and there were some differences among species in their use of thinned forests (Humes, Hayes & Collopy 1999). Another study of thinned, unthinned and intact forests found no difference in bat activity across treatments or among bat species, but the time between thinning and the study was not defined (Kutt 1995).

The purpose of our study was to determine the immediate response of bats to timber harvesting, by testing for differences in foraging by bats in different habitats available in a harvested forest. We investigated habitat use by bats among open, thinned and intact patches. We tested for possible differences in three forest types, deciduous-dominated, conifer-dominated and mixed forests, as structural differences related to forest type (e.g. canopy, understorey) may influence habitat use by bats. Due to differences in manoeuvrability among bat species, when possible we assessed differences among species in their habitat use at all spatial scales. We hypothesized that small, manoeuvrable species would not be influenced by clutter, whereas larger species would be constrained to more open habitat. Consequently, we predicted that larger species would use the centre of patches more than the edges, as edges are more cluttered.

© 2003 British Ecological Society,

Methods and materials

STUDY SITE

Our study took place in the Ecosystem Management by Emulating Natural Disturbance (EMEND) study area (56°40′N and 118°W) located in the boreal forest north of Peace River, Alberta, Canada (see http://www.biology.ualberta.ca/emend/index.htm for details). This area is primarily mesic with considerable standing water in the form of ponds, lakes and streams. The study area is typified by high precipitation (e.g. 386 mm between 1 May and 15 October 2000) and moderate temperatures (mean ± SE temperature 30 min after sunset, June 2000 = 8·6 ± 0·98 °C, July 2000 = 13·5 ± 0·49 °C). The study area has no history of logging; historical disturbance was primarily due to fires.

Three replicates of three forest types were encompassed within a 8·2 × 11·8-km area. The forest types included deciduous-dominant (Ddom), conifer-dominant (Cdom) and mixed-wood (MX). The deciduous-dominant forests primarily consisted of trembling aspen *Populus tremuloides* Michx., with mean tree age ranging from 57 to 93 years. White spruce *Picea glauca* (Moench Voss) was the dominant tree in the conifer-dominant forests and the mean tree age ranged from 73 to 147 years. In the mixed-wood forests, white spruce was more abundant than trembling aspen and mean age of trees ranged between 84 and 145 years. Additional tree species occurred in each forest at low densities, including balsam poplar *Populus balsamifera* L., black spruce *Picea mariana* (Mill.) B.S.P. and lodgepole pine *Pinus contorta* Douglas ex. Loudon. The various forest types were distributed across the study area and distance between stands varied from 0·29 to 9·4 km. Stem density prior to harvesting did not differ significantly among the Ddom (mean ± SE, 1202·4 ± 101·03 stems ha^{-1}), Cdom (973·74 ± 176·29 stems ha^{-1}) and MX (1209·4 ± 155·96 stems ha^{-1}) forest types ($F = 0·56$, d.f. = 2,17, $P = 0·58$). During the winter of 1998–99 harvesting was completed to create a mosaic of open, thinned and intact patches (mean patch size of each treatment was 10 ha) within each forest type. In thinned patches, machine corridors (5 m wide) were cut to allow access by harvesting machines to achieve the prescribed thinning treatment. All trees within the corridors were removed, resulting in 25% removal of trees from the patch. The appropriate percentage of trees was then removed from retention strips (15 m wide) between the corridors to yield the final prescribed treatment. Therefore the thinning process in our study area was not entirely selective, as is often the goal of thinning.

Due to landscape structure, all treatments could not always be encompassed together in each replicate stand. As a result there was a total of five Ddom stands with two to four treatments per stand, five Cdom stands with two to four treatments per stand, and 10 MX stands that each included one to three treatments. Within a given stand, treatments were located adjacent to one another.

STUDY SPECIES

We captured three species of bats in our study area: little brown *Myotis lucifugus* (Le Conte), northern long-eared *M. septentrionalis* (Trouessart) and silver-haired *Lasionycteris noctivagans* (Le Conte). Little brown and northern long-eared bats are similar in body size (mean ± SE forearm length, 38·8 ± 0·17 mm and 37·9 ± 0·63 mm, respectively; Patriquin 2001) but have different wing morphologies. *Myotis septentrionalis* has a lower wing loading and aspect ratio, rendering it more manoeuvrable (Norberg & Rayner 1987), as reflected by its ability to glean insects from foliage (Faure, Fullard & Dawson 1993). *Myotis lucifugus* possesses slightly longer, narrower wings and forages above water or hawks insects when in flight (van Zyll de Jong 1985). *Lasionycteris noctivagans* possesses relatively short, broad wings and is larger (forearm 41·9 ± 0·99 mm; van Zyll de Jong 1985) and heavier than the other species, thus requiring faster flight (Norberg & Rayner 1987). Based on these characteristics, *M. septentrionalis* is the most manoeuvrable and *L. noctivagans* the least.

HABITAT USE

Between 4 June and 16 July 1999, and 1 June and 8 August 2000, we monitored bat activity in various habitat patches in the three forest types. To assess habitat use by foraging bats in open, thinned and intact habitat, we measured relative bat activity in the replicate patches of each type. Because we were unable to compare bat activity before vs. after harvesting, we sampled the replicate stands to account for variation due to factors other than harvesting treatment. We compared activity in harvested patches to that in intact stands in the same year, thus reducing problems caused by between-year variation. We measured bat activity using AnabatII remote systems to detect the echolocation calls of bats. These systems consisted of an AnabatII detector (Titley Electronics, Ballina, Australia) connected to a tape recorder (Optimus CTR-116, RadioShack, Fort Worth, USA) through a delay switch (Titley Electronics), all housed in weatherproof containers and mounted 1 m off the ground to reduce sound attenuation by understorey vegetation. To maximize the sampled volume of air and minimize external noise such as wind, we set the detectors at sensitivity 8 (the maximum is 10) and orientated them at a 45° angle.

Within each of three replicates of the three forest types, we measured bat activity in 0% (clear-cut), 20% (thinned), 50% (thinned) and 100% (intact) retention patches, where percentage retention refers to the percentage of trees left standing after harvesting. We therefore sampled 36 patches. Each patch had a buffer of intact forest around it ranging in width from 59 to 471 m. We sampled in the centre of each patch and on

© 2003 British Ecological Society,

the patch-side of the interface between the buffer and the patch (the edge), as bats tend to forage preferentially along edges (Grindal 1996). We located the edges of intact patches via demarcations placed on the trees indicating the boundaries between the buffer and patch.

Along patch edges we placed bat detectors pointing parallel to the edge to record bats flying along the edge rather than in the middle of the patch. Each thinned patch consisted of machine corridors alternating with retention strips (see above). Machine corridors and retention strips ran perpendicular to the edge we selected for bat monitoring and we placed the detector in the centre of a retention strip to detect bats along the edge across both retention strips and corridors.

We also monitored bats in the centre of patches, at least 50 m from any edge. In thinned patches we again placed the detector in the centre of a retention strip and orientated it perpendicular to the adjacent machine corridor. Detectors at the edge and centre of a patch were orientated in the same direction. Over the two summers, we sampled each location (i.e. edge and centre) of each of the three replicates of patch and forest type (e.g. replicate 1 of 50% Ddom) on 11–14 nights, resulting in a total of 33–42 nights per location–patch–forest type combination.

Each evening, beginning 30 min after sunset, we sampled the four patches (0%, 20%, 50% and 100%) within a given replicate forest. From night to night we rotated among the three forest types. Each night we recorded ambient temperature at 30-min intervals, beginning 30 min after sunset. During 1999 we began monitoring 30 min after sunset and continued for 150 min, which is the period of maximum foraging activity by bats in Alberta at the latitude of our study area (Crampton & Barclay 1998). Occasional monitoring later at night suggested that *L. noctivagans* continued to be active and thus in 2000 we began sampling 30 min after sunset and continued until 1 h before sunrise (i.e. for 280–370 min, depending on time of sunset and sunrise). We did not sample on nights with precipitation as bat activity tends to be greatly reduced (Grindal *et al.* 1992).

Bats produce ultrasonic sounds (echolocation) to gain information about their environment (Griffin, Webster & Michael 1960). We defined each pulse of sound as a call and a series of calls as a pass. When a bat detects a target, such as prey, and approaches it, many calls are produced in rapid succession in a terminal feeding buzz (Griffin, Webster & Michael 1960). We used the number of passes detected per hour of sampling (i.e. pass rate) as an index of relative use of the habitat patches by bats. As a relative measure of feeding activity in the patches, we measured the number of feeding buzzes detected (Griffin, Webster & Michael 1960).

SPECIES IDENTIFICATION

To assess differences in habitat use among different species of bats, we analysed the recorded echolocation calls. We transformed recorded calls to a visual frequency–time display using a zero-crossing analysis interface module (Titley Electronics). For at least some species of bats, echolocation call characteristics are believed to be diagnostic (O'Farrell, Miller & Gannon 1999). To determine which species of bat produced the passes we recorded in the habitat patches, we measured the maximum frequency (the highest frequency of a call), minimum frequency (the lowest frequency of a call) and duration of search phase calls. From these parameters we calculated slope, the difference between the maximum and minimum frequency, divided by duration.

We compared echolocation calls to a library of reference calls collected from individuals identified to species. We obtained the library by recording calls from bats we caught in mist nets. We attached a small chemiluminescent tag (Pucci, Starlite, Brisbane, CA) to the dorsal surface of the bat using surgical glue (Skin-Bond, Smith and Nephew, Largo, FL). After releasing a tagged bat at the capture site, we followed it and recorded its echolocation calls. We obtained calls from five *M. lucifugus*, four *M. septentrionalis* and two *L. noctivagans*, allowing us to account for interindividual variation in call structure (Betts 1998). For the library calls, we measured the same variables as for calls obtained for the habitat-use measures.

We used a multivariate analysis of variance (SAS 8·1, PROC GLM; SAS Institute 1999) to determine which call variables discriminated between species. We then established the values of the variables that bounded values characteristic of a species, and identified the unknown (field) calls using the established thresholds. Calls with a maximum frequency < 60 kHz were removed from analysis as we considered these to be call fragments.

Due to different protocols and weather conditions between years, we tested for a difference in activity rate (passes h^{-1}). There was no significant difference between years and we therefore pooled the data. As low pass rates were common, with some higher values, it was difficult to meet assumptions of normality for statistical tests. Therefore, we first tested for the effect of forest type, patch type and location (edge vs. centre) on the absolute presence of bats, using the proportion of total sampling nights that bats were detected as the dependent variable in a general linear model (SAS 8·1, PROC GLM). To meet assumptions of normality, we arcsine square-root transformed the proportion of nights (Zar 1984).

When bats were present (i.e. nights with no bats detected were removed from the analysis), we tested for the effects of forest type, patch type and location on relative activity of each species or species group using a mixed model (SAS 8·1, PROC MIXED). In this analysis, pass rate was the dependent variable and ambient temperature the covariate. We $\log_{10}$ transformed the data to normalize them. We included forest type, patch type and location as independent variables, replicate as a nested variable within forest type, and patch type by

© 2003 British Ecological Society,

replicate within forest type as a repeated measure in the model. We also included all interaction terms. All non-significant interaction terms were eliminated using hierarchical backwards stepwise elimination. When significant main effects were obtained, we performed relevant post hoc contrasts and adjusted rejection values. To best illustrate the relationships among the data, we present least-squares means ± SE.

Because few feeding buzzes were recorded, we tested for the effect of forest and patch type on the foraging activity of bats (number of observed buzzes) using χ^2 tests. We calculated expected values based on the duration of sampling because sampling effort was not uniform among forest and patch types. In all analyses we used a type I error rate of $\alpha = 0{\cdot}05$.

Results

SPECIES IDENTIFICATION

We detected 459 passes during 214·2 h of sampling in 1999 (2·14 passes h^{-1}) and 1734 passes during 1118·8 h of sampling in 2000 (1·55 passes h^{-1}). Larger species (i.e. primarily *L. noctivagans*) were easily distinguished from smaller species of bats (i.e. *M. lucifugus* and *M. septentrionalis*) based on call characteristics, as larger species had lower maximum and minimum frequencies and longer calls, reflected in a lower slope. Therefore we did not require statistical analysis to distinguish passes of larger bats from those of *Myotis* spp. We recorded some calls not typical of the reference calls for *L. noctivagans* and these may have been produced by big brown bats *Eptesicus fuscus* (Palisot de Beauvois) and hoary bats *Lasiurus cinereus* (Palisot de Beauvois). Reference calls of *E. fuscus* captured in other areas resemble those of our reference calls for *L. noctivagans* (T. Luszcz, personal communication). However, we never captured *E. fuscus* and *L. cinereus* or saw them flying in the area. Although both of these species may have been present in our study area, we conclude that *L. noctivagans* was more abundant and we refer to it in our results.

Calls of *M. lucifugus* and *M. septentrionalis* could be distinguished statistically ($F = 8{\cdot}76$, d.f. = 4,4, $P = 0{\cdot}03$). Both the maximum and minimum frequency were too variable to serve as reliable indicators of species ($F = 1{\cdot}15$, d.f. = 1,7, $P = 0{\cdot}286$; $F = 0{\cdot}13$, d.f. = 1,7, $P = 0{\cdot}723$, respectively), whereas both duration and slope allowed for differentiation between the two *Myotis* spp. ($F = 20{\cdot}66$, d.f. = 1,7, $P < 0{\cdot}001$; $F = 166{\cdot}39$, d.f. = 1,7, $P < 0{\cdot}001$, respectively). As slope incorporates duration, we used slope to distinguish between the two species. *Myotis lucifugus* produced longer, less steep calls than *M. septentrionalis*.

The slope of echolocation calls of *M. lucifugus* ($n = 75$) ranged between 3·5 and 15·9 kHz ms^{-1}, while that of *M. septentrionalis* ($n = 55$) ranged between 8·5 and 27·4 kHz ms^{-1}. These values overlap, so we identified all calls falling within an overlap range simply as *Myotis* spp. We defined *M. lucifugus* calls as those with slopes between 3·5 and 10·9, while *M. septentrionalis* calls fell between 13·0 and 27·4. Nine per cent and 21·8% of *M. lucifugus* and *M. septentrionalis* reference calls, respectively, fell in the unknown range. Only 7% of *M. lucifugus* and *M. septentrionalis* reference calls fell within the range of the other species.

Of the passes we recorded from unknown bats we could identify 29% of all *Myotis* passes; 25% were *Myotis lucifugus* and 4% were *M. septentrionalis*. Due to the low percentage of passes identified to species, we address our hypotheses with respect to small species as a group (*Myotis* spp.) as well as at an individual-species level.

HABITAT USE

Myotis *spp.*

Forest type, patch type and location did not significantly influence the presence or absence of *Myotis* spp. (overall model: $F = 1{\cdot}70$, d.f. = 6,65, $P = 0{\cdot}14$). However, when they were present, their activity varied significantly with forest type ($F = 5{\cdot}74$, d.f. = 2,207, $P = 0{\cdot}004$; Fig. 1). Mean activity rate was higher in conifer

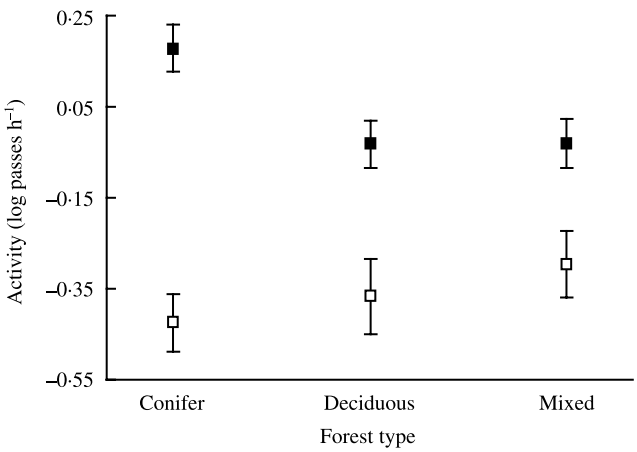

Fig. 1. Least-squares means (± SE) of the log number of *Myotis* spp. (closed symbols) and *Lasionycteris noctivagans* (open symbols) passes detected per hour in three forest types. $n = 33–44$ nights.

© 2003 British Ecological Society,

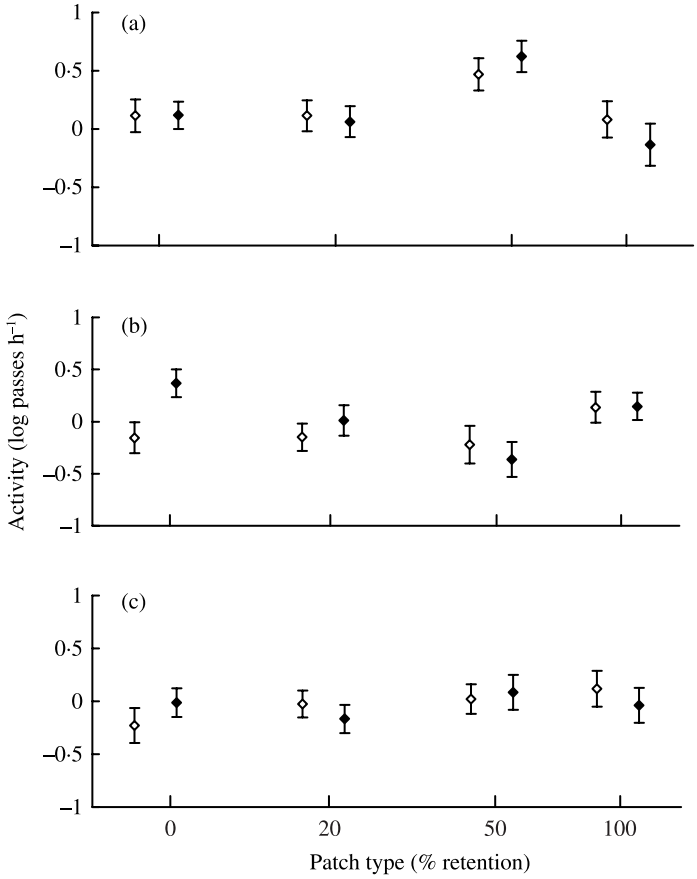

Fig. 2. Least-squares means (± SE) of the log number of *Myotis* spp. passes detected per hour at the edge (closed symbols) and centre (open symbols) of four patch types within (a) Cdom, (b) Ddom and (c) MX stands. n = 11–14 nights.

forests than in deciduous and mixed forests (F = 11·48, d.f. = 1,207, P < 0·001; Fig. 1). The mean pass rate did not differ between deciduous and mixed forests (F = 0·00, d.f. = 1,197, P = 0·97; Fig. 1). *Myotis* spp. activity did not vary significantly among patch types or locations (Fig. 2).

Foraging activity (number of buzzes) of *Myotis* spp. was significantly influenced by forest type, patch type and location. There were more feeding buzzes than expected in deciduous forests (χ^2 = 13·7, d.f. = 3, P < 0·05; Fig. 3), where there were also more buzzes in clear-cuts and intact patches than in the thinned patches (χ^2 = 9·1, d.f. = 1, P < 0·05; χ^2 = 6·4, d.f. = 1, P < 0·05, respectively; Fig. 3). In conifer forests, there were more feeding buzzes than expected in the 20% patches than in the other patch types (χ^2 = 7·5, d.f. = 1, P < 0·05). In mixed forests, there was no effect of patch type on the number of buzzes detected (χ^2 = 3·4, d.f. = 3, P > 0·05; Fig. 3). In the three forest types combined, the number of feeding buzzes was significantly greater at the edge (n = 35 buzzes) than in the centre (n = 2) of clear-cuts (χ^2 = 28·2, d.f. = 1, P < 0·05).

Myotis lucifugus *and* M. septentrionalis

Forest type, patch type and location did not affect the presence of *M. lucifugus* or *M. septentrionalis* (overall models: F = 1·64, d.f. = 6,65, P = 0·15; F = 0·66, d.f. = 6,65, P = 0·68, respectively). Furthermore, in contrast to *Myotis* spp. as a group, the three habitat variables did not significantly influence mean pass rate of either *M. lucifugus* (forest type: F = 0·24, d.f. = 2,113, P = 0·79; patch type: F = 1·58, d.f. = 2, 113, P = 0·20; location: F = 3·20, d.f. = 3,113, P = 0·08; Fig. 4) or *M. septentrionalis* separately (F = 0·01, d.f. = 2,48, P = 0·99; F = 0·53, d.f. = 2,48, P = 0·66; F = 2·33, d.f. = 1,48, P = 0·13, respectively; Fig. 5). Location had a marginal effect on the activity levels of *M. lucifugus*, as they were generally more active along the edge than in the centre of patches (F = 3·20, d.f. = 1,113, P = 0·08; Fig. 4).

Although forest type, patch type and location did not influence activity levels of species of *Myotis*, patch type and location did influence their foraging activity. Within each forest type, patch type influenced the number of *M. lucifugus* feeding buzzes detected [χ^2 = 15·6, d.f. = 3, P < 0·05 (Cdom); χ^2 = 12·3, d.f. = 3, P < 0·05 (Ddom); χ^2 = 8·9, d.f. = 3, P < 0·05 (MX)]. In deciduous forests, *M. lucifugus* foraged significantly more than expected by chance in clear-cuts (n = 11) than in all other patch types combined (n = 9; χ^2 = 9·2, d.f. = 1, P < 0·05). Too few buzzes were detected in the conifer and mixed forests to allow further analysis to determine which patches had higher foraging activity. In the three forest types combined, the number of *M. lucifugus* feeding buzzes was significantly higher

© 2003 British Ecological Society,

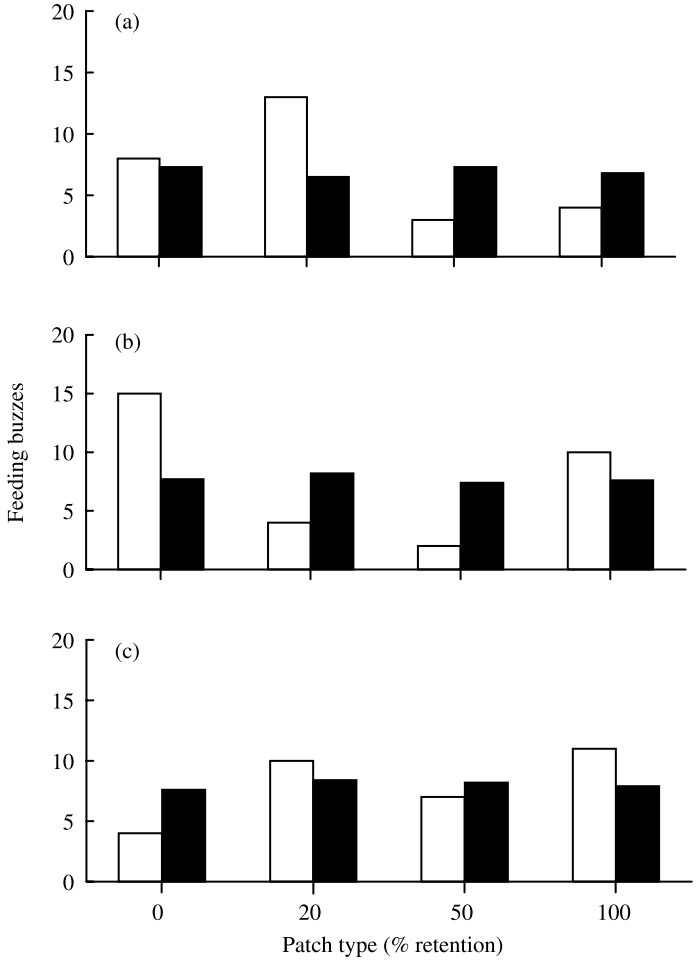

Fig. 3. Total number of observed (open bars) and expected (closed bars) *Myotis* spp. feeding buzzes detected in four patch types within (a) Cdom, (b) Ddom and (c) MX stands. The expected number of buzzes was calculated based on the number of sampling minutes.

along the edge (n = 15) than in the centre (n = 1) of the clear-cuts (χ^2 = 11·7, d.f. = 1, P < 0·05).

There were too few feeding buzzes (n = 11) detected from *M. septentrionalis* to analyse them statistically. However, we did not detect any *M. septentrionalis* passes in the centre of clear-cuts or any *M. septentrionalis* feeding buzzes in either location in the clear-cuts. Most *M. septentrionalis* feeding buzzes (6/11) were recorded in intact patches. The distribution of buzzes among patch types differed significantly between *M. lucifugus* and *M. septentrionalis* (χ^2 = 8·76, d.f. = 3, P < 0·05).

Lasionycteris noctivagans

Forest type and location did not significantly influence the presence of *L. noctivagans* (F = 2·28, d.f. = 2, P = 0·11; F = 0·48, d.f. = 1, P = 0·49, respectively). However, its presence was significantly influenced by patch type (F = 3·06, d.f. = 3,80, P = 0·03). *Lasionycteris noctivagans* was present most often in 0% patches and was absent from intact patches on all but one night. When *L. noctivagans* was present, activity did not differ significantly among forest types (F = 1·48, d.f. = 2,80, P = 0·23; Fig. 1) but did among patch types (F = 3·06, d.f. = 2, 80, P = 0·03; Fig. 6). Activity levels were significantly higher in 0% patches than 20% and 50% patches (F = 7·10, d.f. = 1,77, P = 0·01; Fig. 6). Although activity did not differ significantly with location, there was a trend towards higher activity at the edge of patches (F = 3·39, d.f. = 1,80, P = 0·07). We detected too few feeding buzzes to analyse the influence of habitat types on foraging activity of *L. noctivagans*.

Discussion

The bat community we studied consisted of three species, one larger (*L. noctivagans*) and two smaller (*M. lucifugus* and *M. septentrionalis*). Based on the calls we could identify, we detected far more *M. lucifugus* than *M. septentrionalis*, and thus the *Myotis* spp. category was probably influenced primarily by *M. lucifugus*. Because of the low proportion of *Myotis* calls we could identify to species, sample size for individual *Myotis* species was low and thus the power to detect significant effects was low. None the less, we found that bats in our study area did not use the available habitats equally and, as we predicted, habitat use differed among species and species groups.

The presence of smaller bats (*Myotis* spp.) was not influenced by forest type, patch type or location,

© 2003 British Ecological Society,

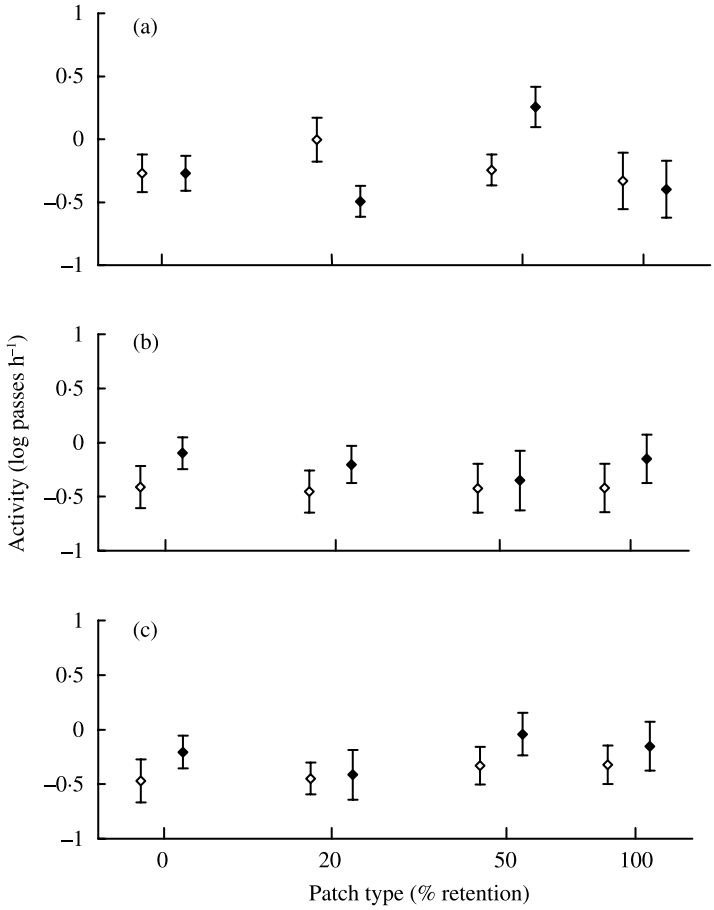

Fig. 4. Least-squares means (± SE) of the log number of *Myotis lucifugus* passes detected at the edge (closed symbols) and centre (open symbols) of four patch types within (a) Cdom, (b) Ddom and (c) MX stands. n = 11–14 nights.

whereas larger bats (*L. noctivagans*) were absent from intact patches and were present most often in clear-cuts (0% patches). Smaller bats were most active in conifer forests, while forest type did not influence the activity of larger bats. Furthermore, patch type and location did not influence the activity of smaller bats, whereas larger bats were more active in clear-cuts than in thinned patches. Together, these results suggest that smaller and larger bats use harvested forests differently; smaller bats in our study were less influenced by clutter than larger bats were.

Our finding that *Myotis* bats were more active in conifer forests compared with other forest types is not consistent with our prediction, or with previous studies (Walsh & Mayle 1991; Walsh & Harris 1996). Other studies suggest that conifer forests offer few foraging opportunities for bats (Thomas 1988; de Jong 1994) and *Myotis* spp. feeding activity in our study was lower in conifer and mixed-wood forests than in deciduous stands. Thus, *Myotis* bats may have been more active in conifer forests because such stands provide resources other than foraging habitat, such as roosts. Many species of bats prefer older trees for roosting sites (Vonhof & Barclay 1996; Crampton & Barclay 1998) and the conifer trees in our study area were generally older (mean age 73–147 year) than the deciduous trees (mean age 57–93 year). However, trees decay at different rates and in mixed-wood forests in Alberta bats prefer to roost in deciduous trees (aspen) rather than conifers (Crampton & Barclay 1998). Unlike the response observed for *Myotis* spp. as a group, *M. lucifugus* and *M. septentrionalis* showed no species-specific preference for forest type, although this may be an artefact of low sample size.

Consistent with previous studies (Erickson & West 1996; Krusic & Neefus 1996), *Myotis* activity was not different among open, thinned or intact patches. This was also reflected in the activity of each species when considered separately. *Myotis lucifugus* feed in and above the canopy (Kalcounis *et al.* 1999) and may use the top of the canopy as a habitat edge, similar to their use of edges in clear-cuts (Bradshaw 1996; Grindal & Brigham 1999). We occasionally visually observed bats flying above the canopy and at the same time detected them with an Anabat detector. Although detection of bats above the canopy might have prevented us from detecting differences in activity among patch types, the relative insensitivity of the Anabat detector compared with other detectors (Fenton *et al.* 2001) makes this unlikely.

Foraging activity of *Myotis* spp. was influenced by vegetation density. *Myotis* spp. as a group, and *M. lucifugus* on its own, foraged more in deciduous clear-cuts, specifically at the edge, and in intact patches. These bats may have been selecting for insect availability as in

© 2003 British Ecological Society,

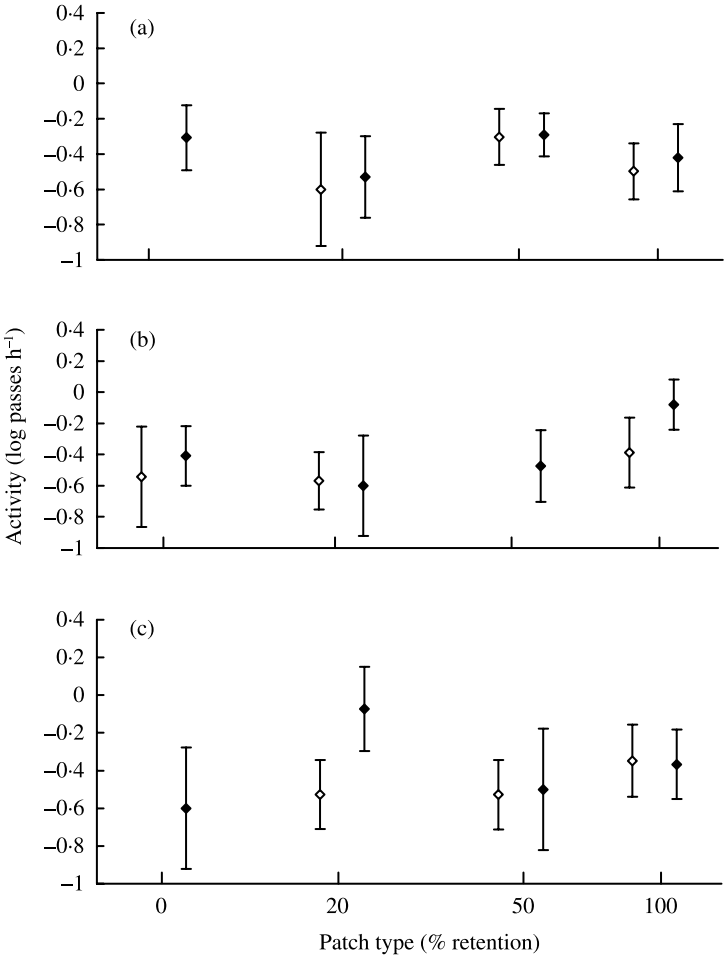

Fig. 5. Least-squares means (± SE) of the log number of *Myotis septentrionalis* passes detected at the edge (closed symbols) and centre (open symbols) of four patch types within (a) Cdom, (b) Ddom and (c) MX stands. n = 11–14 nights.

some areas insects are more abundant in uncut forest and at the edge of clear-cuts than in the centre of clear-cuts (Grindal 1996; Burford, Lacki & Covell 1999) due to passive accumulation at the edge created by wind (Lewis & Stephenson 1966; Lewis 1969, 1970; Lewis & Dibley 1970; Verboom & Spoelstra 1999). Bats may also prefer edges as they provide shelter from wind (Verboom & Spoelstra 1999) and predators, and landmarks for orientation while commuting (Verboom, Boonman & Limpens 1999). *Myotis septentrionalis* did not forage in clear-cuts and was never detected flying through the centre of these patches. Furthermore, *M. septentrionalis* foraged more in intact patches than expected. *Myotis septentrionalis* is capable of gleaning (removing insects from foliage; Faure, Fullard & Dawson 1993) and intact or thinned forest may provide more gleaning opportunities than clear-cuts.

Presence of clutter affected habitat selection by the larger, less manoeuvrable species in our study area (*L. noctivagans*), but not as we predicted. Contrary to our prediction, *L. noctivagans* did not avoid conifer forests. However, within stands vegetation density may have affected habitat selection by *L. noctivagans*, as it preferred open patches over thinned and intact patches. In fact, no *L. noctivagans* was detected in intact patches, with the exception of three passes detected on one night in an intact conifer patch. As in previous studies on larger species of bats (Grindal 1996; Verboom & Huitema 1997), *L. noctivagans* showed no significant preference for the centre over the edge, although there was a trend towards higher use of edges. *Lasionycteris noctivagans* appears to be an edge-adapted species (Fenton 1990) as it can exploit edge habitat but cannot forage in closed habitat. Relative to the more clutter-adapted *Myotis* species, *L. noctivagans* used the centre of open patches more often, suggesting that clutter affects habitat selection more for this species than for *Myotis* spp.

Unlike results obtained by Kutt (1995), logging had different impacts on the bat species we studied in the northern boreal forest. Although openings created by clear-cutting may promote activity of *L. noctivagans*, clear-cutting reduces the activity of *M. septentrionalis*. Furthermore, species use areas within clear-cuts differently. Such differences in habitat use among species must be considered when assessing the impact of a disturbance on habitat selection by bats, as patterns demonstrated by an entire community may not reflect those of individual species. Results can be driven by habitat use of more abundant species, as was observed in our study; *Myotis* spp. activity was influenced most strongly

© 2003 British Ecological Society,

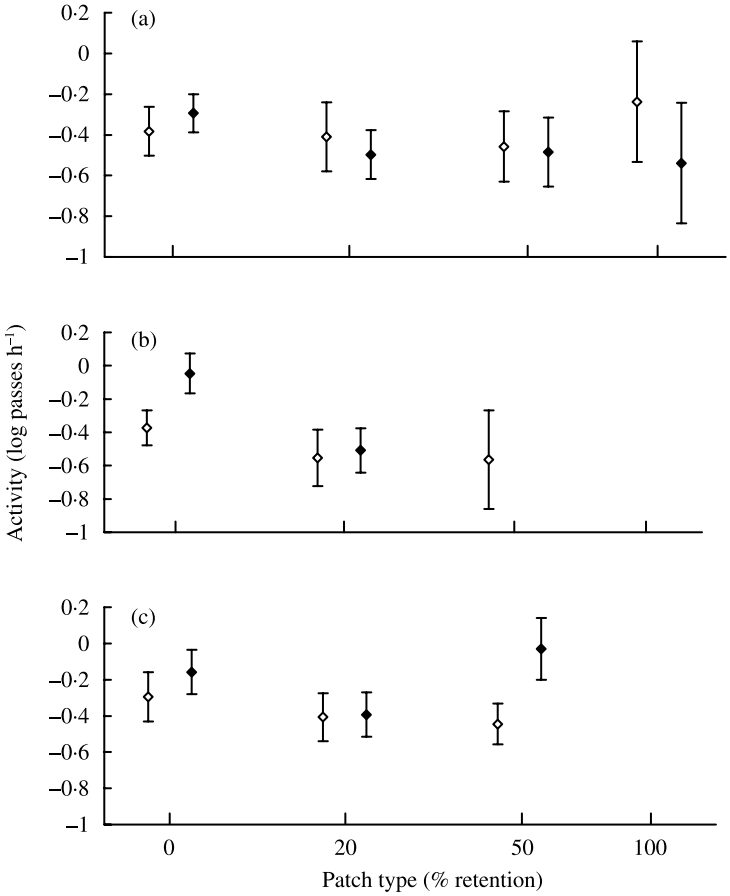

Fig. 6. Least-squares means (± SE) of the log number of *Lasionycteris noctivagans* passes detected at the edge (closed symbols) and centre (open symbols) of four patch types within (a) Cdom, (b) Ddom and (c) MX stands. n = 11–14 nights. Note analyses were performed on means when bats were present, therefore absent data points represent instances when bats were never detected.

by *M. lucifugus*, which was the most commonly detected species. Our results support the hypothesis that discrepancies among studies that have investigated the impact of openings on bat activity are due to different preferences exhibited by the species of interest. Positioning of bat detectors may also influence bat activity interpretations, as bat detectors placed in open flyways yield high activity regardless of logging history (Kutt 1995; Law & Chidel 2002).

Our study provides insight into the immediate impact of logging on selection of foraging habitat by bats in the northern boreal forest. Longer-term studies would provide additional information as the structure of the forests and patches change over time due to loss of trees (from wind-throw), and regeneration. Furthermore, bats show fidelity to foraging grounds (Wai-Ping & Fenton 1989; Audet 1990), suggesting that they may not have discovered the newly created habitat at the time of our study. None the less, the short-term responses we observed illustrate that small, manoeuvrable species were able to exploit all of the habitat available to them in our study area, regardless of the amount of vegetation. Conversely, larger, less manoeuvrable species were confined to more open habitat with little clutter.

Our results also suggest that forest thinning provides minimal immediate benefit to foraging bats. None of the species in our study demonstrated a preference for thinned patches, with the exception of the 20% conifer patches preferred by *Myotis* spp. Over time, thinning might prove more beneficial than clear-cutting for bats, as bat activity in thinned patches can eventually approximate that recorded in old-growth forests (Humes, Hayes & Collopy 1999). Furthermore, many bats also rely on trees for roosting habitat. Roosting habitat is lost through clear-cutting while thinning can potentially allow salvage of this critical habitat, if trees appropriate for roosting are retained. In managing for bats in forests, consideration must be given to the impacts of logging on the selection of foraging habitat by bats and differences among species in habitat selection, as well as the potential influence on roosting habitat availability and quality. A harvesting strategy that creates a mosaic of open, thinned and intact patches may be most suitable. A patchy landscape would accommodate the different needs of the species within the bat community we studied, and would more closely approximate the natural landscape.

Acknowledgements

We thank T. Meldrum, B. Chruszcz and L. Hogberg for assistance in the field, and Daishowa-Marubeni

© 2003 British Ecological Society,

International, Canfor, Estabrook Logging and J. Spence for logistical support. L. Harder provided statistical assistance and L. Harder, R. Longair, C. Gates, B. Law and an anonymous referee made comments that improved the manuscript. The research was funded by grants from Bat Conservation International, the Canadian Circumpolar Institute, the University of Calgary, the Natural Sciences and Engineering Research Council of Canada (NSERC), and the Alberta Conservation Association (Challenge Grants in Biodiversity). K.J. Patriquin was supported by scholarships from NSERC and the University of Calgary.

References

Aldridge, H.D.J.N. & Rautenbach, I.L. (1987) Morphology, echolocation and resource partitioning in insectivorous bats. *Journal of Animal Ecology*, **56**, 763–778.

Altringham, J.D. (1996) *Bats: Biology and Behaviour*. Oxford University Press, Oxford, UK.

Andrén, H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*, **71**, 355–366.

Audet, D. (1990) Foraging behavior and habitat use by a gleaning bat, *Myotis myotis* (Chiroptera: Vespertilionidae). *Journal of Mammalogy*, **71**, 420–427.

Barclay, R.M.R. & Brigham, R.M. (1996) *Bats and Forests Symposium, October 19–21, 1995, Victoria, British Columbia, Canada*. Working Paper 23/1996. Research Branch, British Columbia Ministry of Forests, Victoria, Canada.

Betts, B.J. (1998) Effects of interindividual variation in echolocation calls on identification of big brown and silver-haired bats. *Journal of Wildlife Management*, **62**, 1003–1010.

Bradshaw, P.A. (1996) The physical nature of vertical forest habitat and its importance in shaping bat species assemblages. *Bats and Forests Symposium, October 19–21, 1995, Victoria, British Columbia, Canada* (eds R.M.R. Barclay & R.M. Brigham), pp. 199–212. Working Paper 23/1996. Research Branch, British Columbia Ministry of Forests, Victoria, Canada.

Brigham, R.M., Grindal, S.D., Firman, M.C. & Morissette, J.L. (1997) The influence of structural clutter on activity patterns of insectivorous bats. *Canadian Journal of Zoology*, **75**, 131–136.

Bright, P.W. & Morris, P.A. (1996) Why are dormice rare? A case study in conservation biology. *Mammalian Review*, **26**, 157–187.

Burford, L.S., Lacki, M.J. & Covell, C.V. Jr (1999) Occurrence of moths among habitats in a mixed mesophytic forest: implications for management of forest bats. *Forest Science*, **45**, 323–332.

COSEWIC (2001) Committee on the Status of Endangered Wildlife in Canada, http://www.cosewic.ge.ca.

Crampton, L.H. & Barclay, R.M.R. (1996) Habitat selection by bats in fragmented and unfragmented aspen mixedwood stands of different ages. *Bats and Forests Symposium, October 19–21, 1995, Victoria, British Columbia, Canada* (eds R.M.R. Barclay & R.M. Brigham), pp. 238–259. Working Paper 23/1996. Research Branch, British Columbia Ministry of Forests, Victoria, Canada.

Crampton, L.H. & Barclay, R.M.R. (1998) Selection of roosting and foraging habitat by bats in different-aged aspen mixedwood stands. *Conservation Biology*, **12**, 1347–1358.

Crome, F.H.J. & Richards, G.C. (1988) Bats and gaps: michrochiropteran community structure in a Queensland rain forest. *Ecology*, **69**, 1960–1969.

Erickson, J.L. & West, S.D. (1996) Managed forests in the Western Cascades: the effect of seral stage on bat habitat use patterns. *Bats and Forests Symposium, October 19–21, 1995, Victoria, British Columbia, Canada* (eds R.M.R. Barclay & R.M. Brigham), pp. 215–227. Working Paper 23/1996. Research Branch, British Columbia Ministry of Forests, Victoria, Canada.

Faure, P.A., Fullard, J.H. & Dawson, J.W. (1993) The gleaning attacks of the northern long-eared bat, *Myotis septentrionalis*, are relatively inaudible to moths. *Journal of Experimental Biology*, **178**, 173–189.

Fenton, M.B. (1990) The foraging behaviour and ecology of animal eating bats. *Canadian Journal of Zoology*, **68**, 411–422.

Fenton, M.B., Bouchard, S., Vonhof, M.J. & Zigouris, J. (2001) Time-expansion and zero-crossing period meter systems present significantly different views of echolocation calls of bats. *Journal of Mammalogy*, **82**, 721–727.

Griffin, D.R., Webster, F.A. & Michael, C.R. (1960) The echolocation of flying insects by bats. *Animal Behaviour*, **8**, 141–154.

Grindal, S.D. (1996) Habitat use by bats in fragmented forests. *Bats and Forests Symposium, October 19–21, 1995, Victoria, British Columbia, Canada* (eds R.M. R. Barclay & R.M. Brigham), pp. 260–272. Working Paper 23/1996. Research Branch, British Columbia Ministry of Forests, Victoria, Canada.

Grindal, S.D. & Brigham, R.M. (1998) Short-term effects of small-scale habitat disturbance on activity by insectivorous bats. *Journal of Wildlife Management*, **62**, 996–1003.

Grindal, S.D. & Brigham, R.M. (1999) Impacts of forest harvesting on habitat use by foraging insectivorous bats at different spatial scales. *Écoscience*, **6**, 25–34.

Grindal, S.D., Collard, T.S., Brigham, R.M. & Barclay, R.M.R. (1992) The influence of precipitation on reproduction by *Myotis* bats in British Columbia. *American Midland Naturalist*, **128**, 339–344.

Hansson, L. (1992) Landscape ecology of boreal forests. *Trends in Ecology and Evolution*, **7**, 299–302.

Hayes, J.P. & Adams, M.D. (1996) The influence of logging riparian areas on habitat utilization by bats in western Oregon. *Bats and Forests Symposium, October 19–21, 1995, Victoria, British Columbia, Canada* (eds R.M.R. Barclay & R.M. Brigham), pp. 228–237. Working Paper 23/1996. Research Branch, British Columbia Ministry of Forests, Victoria, Canada.

Humes, M.L., Hayes, J.P. & Collopy, M.W. (1999) Bat activity in the thinned, unthinned, and old-growth forests in western Oregon. *Journal of Wildlife Management*, **63**, 553–561.

Jones, G. & Rayner, J.M.V. (1991) Flight performance, foraging tactics and echolocation in the trawling insectivorous bat *Myotis adversus* (Chiroptera: Vespertilionidae). *Journal of Zoology, London*, **225**, 393–412.

de Jong, J. (1994) Habitat use, home-range and activity patterns of the northern bat, *Eptesicus nilssoni*, in a hemiboreal coniferous forest. *Mammalia*, **58**, 535–548.

Kalcounis, M.C. & Brigham, R.M. (1995) Secondary use of aspen cavities by tree-roosting big brown bats. *Journal of Wildlife Management*, **62**, 603–611.

Kalcounis, M.C., Hobson, K.A., Brigham, R.M. & Hecker, K.R. (1999) Bat activity in the boreal forest: importance of stand type and vertical strata. *Journal of Mammalogy*, **80**, 673–682.

Kavanagh, R.P. & Bamkin, K.L. (1995) Distribution of nocturnal forest birds and mammals in relation to the logging mosaic in south-eastern New South Wales, Australia. *Biological Conservation*, **71**, 41–53.

Krusic, R.A. & Neefus, C.D. (1996) Habitat association of bat species in the White Mountain National Forest. *Bats and Forests Symposium, October 19–21, 1995, Victoria, British Columbia, Canada* (eds R.M.R. Barclay & R.M. Brigham), pp. 185–198. Working Paper 23/1996. Research Branch, British Columbia Ministry of Forests, Victoria, Canada.

© 2003 British Ecological Society,

Kutt, A.S. (1995) Activity and stratification of microchiropteran bat communities in thinned, unthinned and old lowland regrowth forest, East Gippsland. *Victorian Naturalist*, **112**, 86–92.

Law, B.S. (1996) The ecology of bats in south-east Australian forests and potential impacts of forestry practices: a review. *Pacific Conservation Biology*, **2**, 363–374.

Law, B.S. & Anderson, J. (2000) Roost preferences and foraging ranges of the eastern forest bat *Vespadelus pumilus* under two disturbance histories in northern New South Wales, Australia. *Austral Ecology*, **25**, 352–367.

Law, B.S. & Chidel, M. (2002) Tracks and riparian zones facilitate the use of Australian regrowth forest by insectivorous bats. *Journal of Applied Ecology*, **39**, 605–617.

Law, B.S., Anderson, J. & Chidel, M. (1999) Bat communities in a fragmented forest landscape on the south-west slopes of New South Wales, Australia. *Biological Conservation*, **88**, 333–345.

Lewis, T. (1969) The distribution of flying insects near a low hedgerow. *Journal of Applied Ecology*, **6**, 443–452.

Lewis, T. (1970) Patterns of distribution of insects near a windbreak of tall trees. *Annals of Applied Biology*, **65**, 213–220.

Lewis, T. & Dibley, G.C. (1970) Air movement near windbreaks and a hypothesis of the mechanism of the accumulation of airborne insects. *Annals of Applied Biology*, **66**, 477–484.

Lewis, T. & Stephenson, J.W. (1966) The permeability of artificial windbreaks and the distribution of flying insects in the leeward sheltered zone. *Annals of Applied Biology*, **58**, 355–363.

Limpens, H.J.G.A. & Kapteyn, K. (1991) Bats, their behaviour and linear landscape elements. *Myotis*, **29**, 39–48.

Mackey, R.L. & Barclay, R.M.R. (1989) The influence of physical clutter and noise on the activity of bats over water. *Canadian Journal of Zoology*, **67**, 1167–1170.

Menzel, M.A., Carter, T.C., Menzel, J.M., Ford, W.M. & Chapman, B.R. (2002) Effects of group selection silviculture in bottomland hardwoods on the spatial activity patterns of bats. *Forest Ecology and Management*, **162**, 209–218.

Norberg, U.M. (1981) Wing form and flight mode in bats. *Recent Advances in the Study of Bats* (eds M.B. Fenton, P. Racey & J.M.V. Rayner), pp. 43–56. Cambridge University Press, Cambridge, UK.

Norberg, U.M. & Rayner, J.M.V. (1987) Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London Series B*, **316**, 335–427.

O'Farrell, M.J., Miller, B.W. & Gannon, W.L. (1999) Qualitative identification of free-flying bats using the Anabat detector. *Journal of Mammalogy*, **80**, 11–23.

Parker, D.I., Cook, J.A. & Lewis, S.W. (1996) Effects of timber harvest on bat activity in southeastern Alaska's temperate rainforests. *Bats and Forests Symposium, October 19–21, 1995, Victoria, British Columbia, Canada* (eds R.M.R. Barclay & R.M. Brigham), pp. 277–292. Working Paper 23/1996. Research Branch, British Columbia Ministry of Forests, Victoria, Canada.

Patriquin, K.J. (2001) *Ecology of a bat community in harvested boreal forest in northwestern Alberta*. MSc Thesis. University of Calgary, Calgary, Canada.

Pavey, C.R. & Burwell, C.J. (2000) Foraging ecology of three species of hipposiderid bats in tropical rainforest in northeast Australia. *Wildlife Research*, **27**, 283–287.

Perdue, M. & Steventon, J.D. (1996) Partial cutting and bats: a pilot study. *Bats and Forests Symposium, October 19–21, 1995, Victoria, British Columbia, Canada* (eds R.M.R. Barclay & R.M. Brigham), pp. 273–276. Working Paper 23/1996. Research Branch, British Columbia Ministry of Forests, Victoria, Canada.

Robinson, W.D. & Robinson, S.K. (1999) Effects of selective logging on forest bird populations in a fragmented landscape. *Conservation Biology*, **13**, 58–66.

SAS Institute (1999) *SAS System for Windows, version 8·1*. SAS Institute, Cary, north Carolina, USA.

Schieck, J., Lertzman, K., Nyberg, B. & Page, R. (1995) Effects of patch size on birds in old-growth montane forests. *Conservation Biology*, **9**, 1072–1084.

Stelfox, J.B. (1995) Introduction. *Relationships Between Stand Age, Stand Structure, and Biodiversity in Aspen Mixedwood Forests in Alberta* (ed. J.B. Stelfox), pp. 1–12. Alberta Environmental Centre (AEC V95-R1), Vegreville, and Canadian Forest Service (Project No. 0001A), Edmonton, Canada.

Thomas, D.W. (1988) The distribution of bats in different ages of Douglas-fir forests. *Journal of Wildlife Management*, **52**, 619–626.

Tuttle, M.D. & Stevenson, D. (1982) Growth and survival of bats. *Ecology of Bats* (ed. T.H. Kunz), pp. 105–150. Plenum Press, New York, NY.

Verboom, B. & Huitema, H. (1997) The importance of linear landscape elements for the pipistrelle *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*. *Landscape Ecology*, **12**, 117–125.

Verboom, B. & Spoelstra, K. (1999) Effects of food abundance and wind on the occurrence of pipistrelle bats *Pipistrellus pipistrellus* and serotines *Eptesicus serotinus* near treelines. *Canadian Journal of Zoology*, **77**, 1393–1401.

Verboom, B., Boonman, A. & Limpens, H.J.G.A. (1999) Acoustic perception of landscape elements by echolocating pond bats (*Myotis dasycneme*). *Journal of Zoology, London*, **248**, 59–66.

Vonhof, M.J. & Barclay, R.M.R. (1996) Roost-site selection and roosting ecology of forest-dwelling bats in southern British Columbia. *Canadian Journal of Zoology*, **74**, 797–1805.

Wai-Ping, V. & Fenton, M.B. (1989) Ecology of spotted bat (*Euderma maculatum*) roosting and foraging behavior. *Journal of Mammalogy*, **70**, 617–622.

Walker, D., Stelfox, J.B., Wasel, S. & Hebert, D. (1996) Natural disturbance regimes as templates for boreal forest harvest. *Bats and Forests Symposium, October 19–21, 1995, Victoria, British Columbia, Canada* (eds R.M.R. Barclay & R.M. Brigham), pp. 3–18. Working Paper 23/1996. Research Branch, British Columbia Ministry of Forests, Victoria, Canada.

Walsh, A.L. & Harris, S. (1996) Foraging habitat preference of vespertilionid bats in Britain. *Journal of Applied Ecology*, **33**, 508–518.

Walsh, A.L. & Mayle, B.A. (1991) Bat activity in different habitats in a mixed lowland woodland. *Myotis*, **29**, 97–104.

Zar, J.H. (1984) *Biostatistical Analysis*, 2nd edn. Prentice Hall, NJ.

van Zyll de Jong, C.G. (1985) *Handbook of Canadian Mammals*. National Museums of Natural Science, Ottawa, Canada.

Received 2 July 2002; final copy received 20 March 2003

© 2003 British Ecological Society,