

# Habitat Use by Bats in Fragmented Forests

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## ABSTRACT

Habitat disturbance associated with forest harvesting has various effects on wildlife. To assess the impact on bats, I used ultrasonic detectors to monitor relative habitat use by bats in disturbed forested sites and riparian areas. In addition, I experimentally tested the effect of spatial clutter on the foraging activity of bats. My results suggest that habitat use by foraging bats varies depending on a combination of spatial clutter and prey availability. In forested areas, clear-cut edges appeared to be preferred foraging sites. However, much greater foraging rates were observed in habitats associated with lakes. Activity patterns and prey availability levels in forest suggested that this habitat type may be important for roosting and as a source of prey. Therefore, the creation of preferred foraging habitat by forest harvesting must be balanced with the removal of other requirements (e.g., tree roost sites), as well as protection of primary foraging areas (lakes).

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## INTRODUCTION

Habitat may be disturbed in a number of ways. Intensive agriculture alters large areas of habitat. Wildfires may also affect large areas, and are thought to be regulating influences in some ecosystems. Forest harvesting is another form of habitat disturbance, and is now one of the major kinds of large-scale disturbances occurring in forest ecosystems.

In the past, the forest industry has not had the best reputation for considering forest resource values, other than timber. However, recent emphasis has been placed on non-timber forest values, such as wildlife. Forest companies now protect wildlife habitat, including wildlife trees, which are saved for their potential shelter and food. Yet, problems still exist with integrating forestry practices and wildlife habitat requirements in an ecosystem context (Hunter 1990).

Large-scale habitat disturbances cause abiotic changes in the environment (e.g., direct loss of habitat or changes in microclimate conditions). Changes in abiotic conditions may in turn affect biotic components of the environment, such as prey availability, competition between and within species, or predation rates. These changes resulting from habitat disturbances may then affect animals in a number of ways, depending on the nature of the disturbance, and on the ecology of the particular species

(Pickett and White 1985). For example, forest harvesting may have positive, negative, or neutral impacts on wildlife, affecting such things as foraging success, which may in turn influence population dynamics. Previous studies suggest that some animals may benefit from forest harvesting (Sparks et al. 1994), whereas others may be negatively influenced (Chubbs et al. 1992). For other species, there appears to be no dramatic impact on their ecology (Medin 1986).

Unlike many other vertebrates, there is a limited amount of information on the effects of forest harvesting on bats. Most of the previous work on the ecology of bats has been conducted in caves or human-made structures, and very little is known about what role bats may play in a forest ecosystem, and the effects of large-scale disturbances.

Two basic requirements of bats are roosting and foraging habitat. Roosting habitat provides areas for shelter during the day and for reproduction, whereas foraging habitat provides for energy and nutrient requirements. If bats have specific tree-roost requirements, then forest harvesting would have an obvious negative impact on roosting ecology. However, the impact of forest harvesting on the foraging ecology of bats is not as evident. Forest harvesting creates openings in the forest, and previous studies suggest that gaps and the resulting edge habitat are important foraging areas for some bat species (Fenton 1990).

For my purposes, forest harvesting results in three distinct habitat types. The first are clearcuts, which represent disturbed habitat where the majority of the vegetation is removed. The second is edge, which represents the boundary between clearcuts and the remaining forest. The third is forest, which represents undisturbed habitat.

As a result of forest harvesting, bats are presented with a choice of the three different habitat types. Bats may select certain foraging habitats depending on the physical nature of the habitat and/or the prey availability found there. Habitat selection may also be determined to some extent by the ecomorphology of the animal. Ecomorphology can be defined as aspects of an organism's ecology that may be dictated by certain morphological features (Findley 1993).

For bats, I have used three characteristics to describe their ecomorphology. The first is the size of the bat, which will determine the size of prey that can be consumed. The second is wing loading, which deals with the mass and wing area of bats. These two characteristics can be used to predict habitat use by bats over a continuum ranging from large, fast-flying bats to small, slow-flying bats that are more agile. The third characteristic is echolocation, which is the mechanism that bats use to perceive their environment and search for prey (Griffin 1958). Different bats produce different frequencies of echolocation, which allows for varying trade-offs between such things as range of detection and resolution (Norberg 1987; Norberg and Rayner 1987). That is, large, fast-flying, less manoeuvrable bats tend to have echolocation that permits long-range detection of objects (over 5 m), but with a relatively coarse resolution of environmental detail. These bats should be limited to relatively open habitat. In contrast, small, slow-flying, agile bats have echolocation that permits fine resolution of the environment, but at a short range (1–2 m). These bats should be able to fly and navigate in more cluttered or environmentally complex habitats, but not be restricted to them.

Predictions

Insects are the exclusive prey of bats in Canada (van Zyll de Jong 1985), and this prey base may vary between different habitats. I hypothesized that the foraging activity of different types of bats should vary depending on the degree of spatial complexity of a habitat (i.e., clutter; Figure 1), and on prey availability. Specifically, dealing with only the degree of clutter of a habitat, I predicted that the open-adapted bats (large, fast-flying, less manoeuvrable) should be limited to clear-cut areas, with reduced activity in the more cluttered habitat of the forest. In contrast, clutter-adapted bats (small, slow-flying, and more manoeuvrable) should not be limited to specific foraging areas, and therefore should display relatively equal activity patterns across the three habitat types (see also Fenton 1990).

The purpose of my study was to monitor habitat use by foraging bats in areas associated with forest harvesting and in riparian habitat. In addition, I experimentally tested the effect of spatial clutter on the foraging activity of bats.

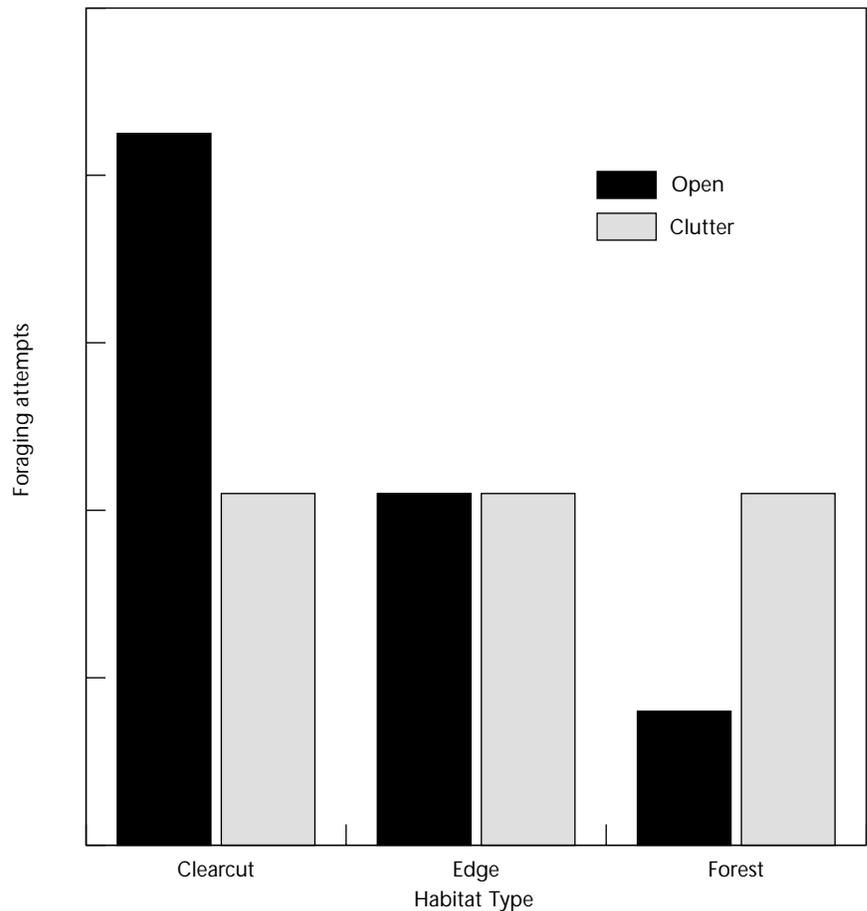


FIGURE 1 Predicted foraging activity for open-adapted bats (open) and clutter-adapted bats (clutter) in the three habitat types associated with clear-cuts. Note that the predicted values are relative, not absolute.

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Study Site	<p>The study took place during the summers of 1993–1995 in the West Arm Demonstration Forest in the southern interior of British Columbia. The study site is approximately 14,500 ha, encompassing five watersheds that drain into Kootenay Lake. The area is dominated by conifers, and elevation ranges from 540 m at Kootenay Lake to 1800 m in the subalpine.</p>
Sampling of Clearcuts	<p>To monitor relative bat activity in habitat types associated with clearcuts, I used Mini-2 ultrasonic bat detectors (Ultra Sound Advice, U.K.) for 90 minutes after sunset (Pacific Standard Time). The detectors were connected to micro-cassette recorders to allow for multiple sampling, as well as transcription of bat activity over certain time periods.</p> <p>Overall bat activity was separated into two activity types: commuting and foraging. Commuting activity was identified by a steady series of echolocation calls (two or more consecutive pulses; Thomas 1988), emitted when bats are searching for prey or travelling. Foraging activity was identified by a rapid series of echolocation calls or a “feeding buzz,” produced when bats make a feeding attempt (Griffin 1958).</p> <p>Bat activity was separated into two species groups as either clutter-adapted (detectors set at 40 kHz) or open-adapted (detectors set at 25 kHz) bats. The two groups were differentiated based on the frequency setting of the detectors, as well as pulse repetition rate (Thomas and West 1989). Bats that were expected in the study area were categorized as either clutter-adapted (<i>Myotis californicus</i>, <i>M. evotis</i>, <i>M. lucifugus</i>, <i>M. septentrionalis</i>, <i>M. volans</i>, <i>M. yumanensis</i>) or open-adapted (<i>Eptesicus fuscus</i>, <i>Lasionycteris noctivagans</i>, <i>Lasiurus cinereus</i>; Nagorsen and Brigham 1993).</p> <p>To assess insect availability, I used light-suction traps (Kunz 1988) paired with bat detectors. Insect biomass was determined by drying a representative sample of insects to a constant mass at room temperature. The mean mass for each insect order was then multiplied by the number caught in each habitat type per sample night.</p> <p>On a sample night, one pair of bat detectors (40 and 25 kHz) and a light-suction trap were placed in each of the three habitat types associated with clearcuts (clearcut, edge, and forest). To maintain independence of observation and eliminate any edge effects (Sisk and Margules 1993), bat detectors and insect traps were placed at least 50 m into forest and clearcut habitat types. Samples were taken randomly throughout the summers of 1993 and 1994.</p>
Clutter Sampling	<p>To experimentally test for the effect of spatial complexity of a habitat on the foraging activity of bats, I constructed areas of artificial clutter, or “clutter boxes.” These clutter boxes consisted of a cube-shaped area extending from the edge of a clearcut (30 m along the edge of the clearcut × 20 m out from the edge × 18 m above the ground). The spatial clutter consisted of over 5500 m of suspended twine for each clutter box (one vertical line every 1 m). Foraging activity and insect availability were monitored using a similar protocol as in the clearcut sampling. Bat detectors and insect traps were placed inside the clutter box (treatment), and farther along the edge of the same clearcut (control). Two complete set-ups</p>

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(treatment and control) were constructed. Samples were taken at approximately weekly intervals throughout the summer of 1995.

Lake Sampling To assess the importance of riparian habitat, I sampled bat foraging activity in lake areas. A similar protocol was used as in the clearcut sampling (i.e., centre of the lake, edge of the lake, and adjacent forest). However, detectors in the centre of the lake were placed in plastic containers and floated out onto the lakes in small inner-tubes. Samples were taken in July 1994, and at approximately monthly intervals throughout the summer of 1995.

Statistical Analyses I used Kruskal-Wallis one-way analysis of variance (Zar 1984) to examine the effect of bat type and habitat type on foraging activity and insect availability (excluding bat type for the latter). In cases of a significant effect, I conducted non-parametric multiple comparisons (Dunn procedure; Zar 1984). Proportional data were arcsine-transformed prior to statistical analysis. Spearman Rank correlation tests were used to examine the relationship between insect availability and foraging activity. I used a rejection level of 0.05 in all cases.

## RESULTS

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Clearcut Sampling I collected 693 hours of bat activity data in the three habitat types on a total of 77 nights. These data consisted of 192 foraging attempts and 2024 commuting passes. Habitat type had a significant effect on overall bat foraging activity (Figure 2, Table 1). Foraging activity was significantly greater along the edge than in the clearcut or forest habitat for clutter-adapted bats. Open-adapted bats showed a similar pattern, except that foraging activity did not differ significantly between the clearcut and edge. As predicted, open-adapted bats foraged significantly more than the clutter-adapted bats in the less spatially complex habitat type of the clearcut. However, foraging activity between the two bat types did not differ in the other two habitat types.

Both types of bats foraged infrequently in the forest. In 231 hours of observation, I recorded no foraging attempts by open-adapted bats in the forest, and only one by a clutter-adapted bat. However, commuting activity was recorded in the forest, suggesting that bats do use this habitat type (Figure 3). Commuting activity in the forest peaked between 20 to 30 minutes after sunset, then remained consistently low (Figure 3). Commuting activity in the edge and clearcut tended to be greater, and peaked later, than activity in the forest. A similar trend was observed for foraging activity, with the exception of only a single foraging attempt recorded in the forest.

I sampled for a total of 432 hours using insect light-suction traps on 48 nights during 1994. In all, this sampling resulted in the capture of 2424 insects. Habitat type had a significant effect on insect availability (Figure 4). Total insect biomass was significantly less in clearcut than edge or forest habitats (for both,  $H = 4.01$ ,  $df = 1,96$ ,  $p < 0.05$ ), and did not differ significantly between the edge and forest ( $H = 0.09$ ,  $df = 1,96$ ,  $p > 0.05$ ). Total mean insect biomass from all habitat types contained predominantly

TABLE 1 *Kruskal-Wallis test results for bat foraging activity associated with clearcuts and lakes.*

Variable	Clearcut sampling			Lake sampling		
	df	H or q	p	df	H or q	p
<b>Bat type</b>						
<i>Clearcut/lake</i>						
Open vs. clutter	1,154	6.59	**	1,24	10.11	**
<i>Edge</i>						
Open vs. clutter	1,154	0.0037	>0.5	1,24	1.08	>0.1
<i>Forest</i>						
Open vs. clutter	1,154	1.0	>0.01	1,24	0.032	>0.5
<b>Habitat type</b>						
<i>Open</i>						
Edge vs. forest	1,154	21.44	***	1,24	21.44	***
Edge vs. clearcut/lake	1,154	3.22	>0.05	1,24	2.82	>0.05
Clearcut/lake vs. forest	1,154	11.75	***	1,24	13.46	***
<i>Clutter</i>						
Edge vs. forest	1,154	17.19	***	1,24	20.82	***
Edge vs. clearcut/lake	1,154	14.95	***	1,24	7.3	**
Clearcut/lake vs. forest	1,154	0.33	>0.5	1,24	28.18	***

H represents test values for main effects; q represents test values for multiple comparisons (Dunn's test) when appropriate; \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ . See figures 2 and 7.

Diptera (61.5%) and Lepidoptera (36.5%), with smaller amounts of Hymenoptera, Trichoptera, Neuroptera, Coleoptera, and Hemiptera (combined 2.0%). Mean insect biomass was not significantly correlated to foraging activity (Spearman,  $r = -0.03$ ,  $p > 0.5$ ).

#### Clutter Sampling

In the experimental sites, I collected 34 samples on 17 nights. Mean foraging activity in the clutter box was significantly less than along the edge for clutter-adapted bats ( $H = 6.44$ ,  $df = 1,34$ ,  $p < 0.02$ ), but not for open-adapted bats ( $H = 0.0$ ,  $df = 1,34$ ,  $p = 1.0$ ; Figure 5). Mean insect biomass collected did not differ between the treatment and the control ( $H = 0.058$ ,  $df = 1,34$ ,  $p = 0.81$ ; Figure 6).

#### Lake Sampling

I sampled nine different lakes on 12 nights. Foraging activity in lake areas showed similar patterns to that of the clearcut. Foraging activity by both bat types was significantly greater in the lake and edge habitat than in the forest (Figure 7, Table 1). In particular, foraging activity in the centre of the lake by clutter-adapted bats was significantly greater than open-adapted bats (Figure 7, Table 1), or in the other habitat types. Mean foraging activity for all habitat types associated with lakes was approximately 39 times greater than for those associated with clearcuts.

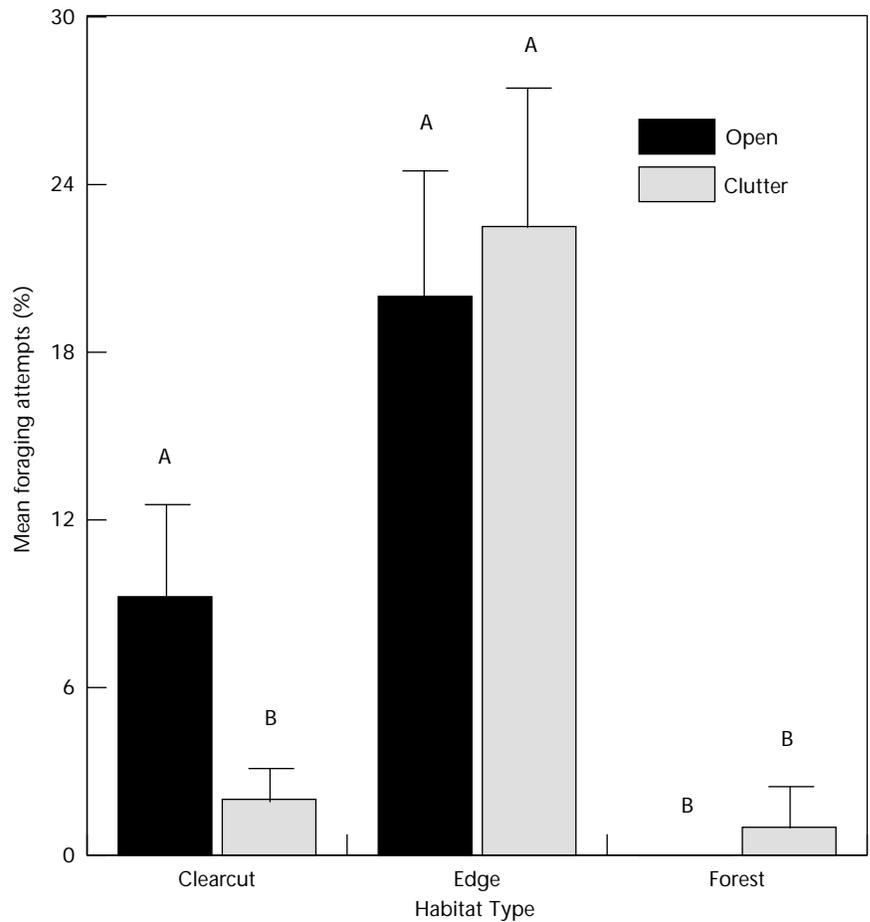


FIGURE 2 Mean (+ 1 SE) foraging activity per hour for open-adapted bats (open) and clutter-adapted bats (clutter) in the three habitat types associated with clearcuts. Within each habitat type, and between habitat types for the same bat type, means with the same letter are not significantly different ( $p > 0.05$ ). See Table 1.

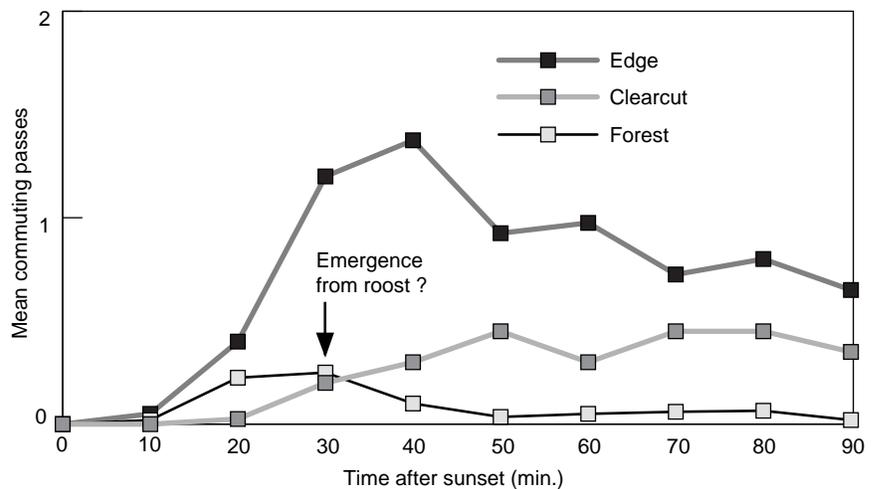


FIGURE 3 Mean commuting activity over time for the three habitat types associated with clearcuts. Bat types were combined.

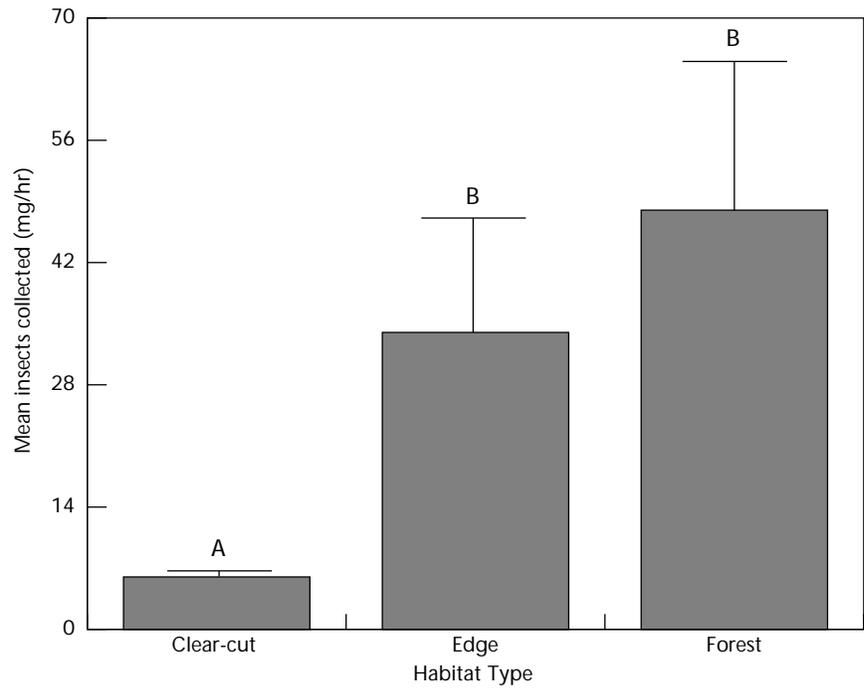


FIGURE 4 Mean (+ 1 SE) insect biomass collected per hour in the three habitat types associated with clearcuts. Means with the same letter are not significantly different ( $p > 0.05$ ).

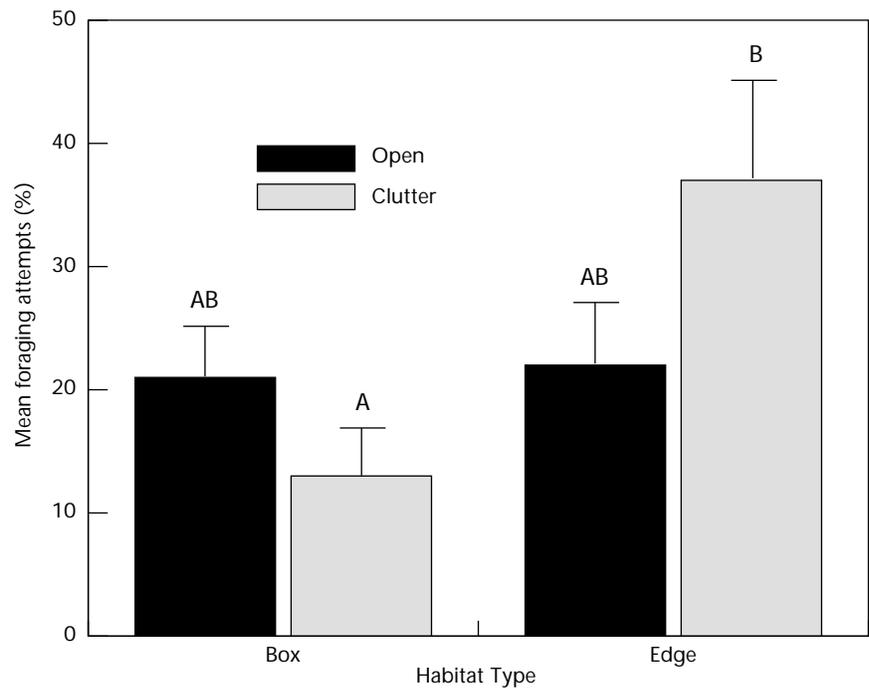


FIGURE 5 Mean (+ 1 SE) foraging activity per hour for open-adapted bats (open) and clutter-adapted bats (clutter) in the clutter box and edge. Within each habitat type, and between habitat types for the same bat type, means with the same letter are not significantly different ( $p > 0.05$ ).

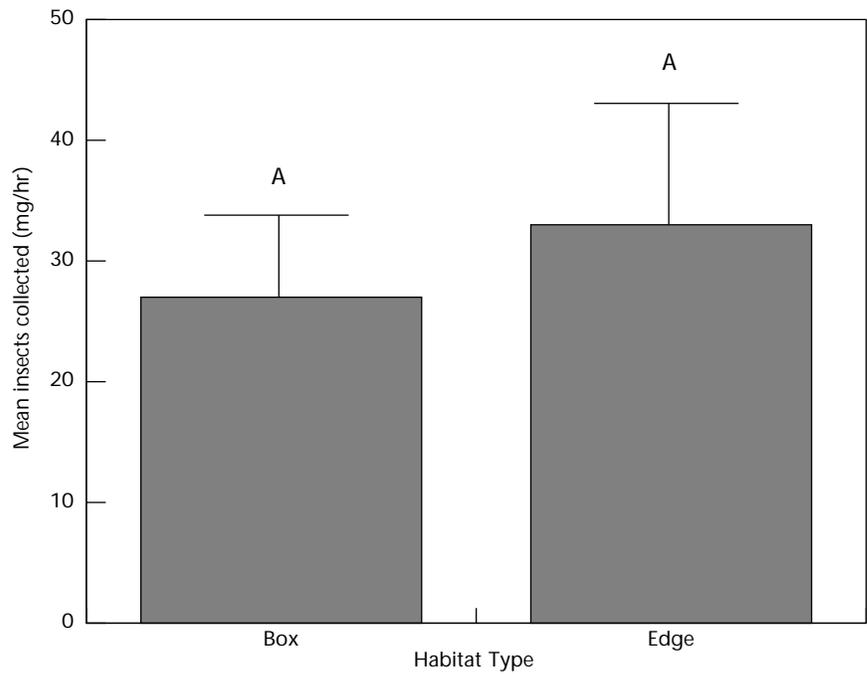


FIGURE 6 Mean (+ 1 SE) insect biomass collected per hour in the clutter box and the edge. Means with the same letter are not significantly different ( $p > 0.05$ ).

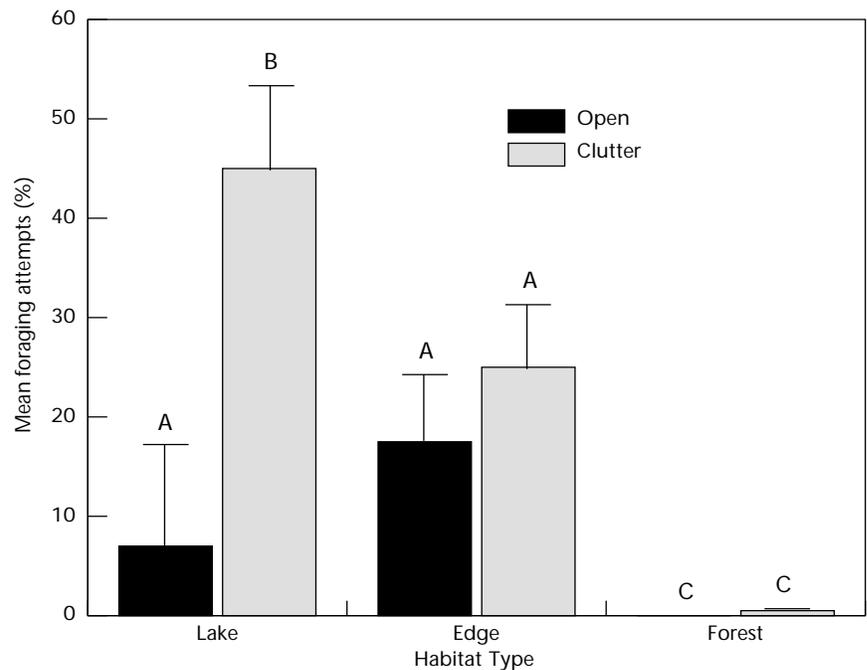


FIGURE 7 Mean (+ 1 SE) foraging activity per hour for open-adapted bats (open) and clutter-adapted bats (clutter) in the three habitat types associated with lakes. Within each habitat type, and between habitat types for the same bat type, means with the same letter are not significantly different ( $p > 0.05$ ). See Table 1.

## Sampling of Clearcuts

My results support the hypothesis that foraging activity of different types of bats varies depending on a combination of habitat structure and prey availability. The patterns observed between the open and clutter bats within each habitat type were as I predicted. Open-adapted bats were significantly more active than clutter-adapted bats in clearcuts, with similar trends for the other habitat types. However, the results between habitat types were not as predicted. Foraging activity was significantly greater on the edge than in the clearcut or forest habitats. Edge may be preferred because of the nature of its vertical structure, which is a relatively unique landscape-form in a forest, and may be used as a navigational reference or flight corridor by bats. There was reduced foraging in the clear-cut areas, yet this habitat type may be important for the larger open-adapted bats, because few obstructions are encountered there. The low activity observed in the forest suggests that this habitat is not an important foraging area for either group of bats, perhaps because of the greater spatial complexity that may make flight and foraging energetically more expensive for bats (Aldridge and Rautenbach 1987; Norberg and Rayner 1987).

The second part of my hypothesis stated that bat activity in the different habitat types should vary depending on prey availability. That is, bats should be most active where there are the most prey. However, my results did not support this prediction. Bat activity was not correlated with insect availability. The edge and forest had significantly greater total insect biomass than the clearcut, which may explain the high bat activity along the edge of clearcuts. Forest habitat appears to be an important source of prey, but may not be an important foraging area for bats because of the greater environmental clutter associated with it. That is, even though there were high prey resources in the forest, the greater degree of clutter prevented bats from using this prey source. Therefore, the preference of bats for edge habitat may be due to a combination of high prey resources, associated with the forest, and the structural nature of edge that provides a navigational reference or flight corridor.

Minimal foraging activity was observed in the forest (i.e., only one foraging attempt recorded in two years). However, commuting activity was detected, suggesting that bats were active in this habitat type. What, then, were bats doing in the forest? Bats roost in hollows or under loose bark of trees (Nagorsen and Brigham 1993). The commuting activity in the forest may be associated with the emergence of bats from their roosts as they travel to other foraging areas. Commuting activity in the forest peaked 30 minutes after sunset, then remained consistently low. This peak in activity may represent the time when bats emerged from their roosts and commuted to foraging areas. This suggests that although the forest habitat may not be an important foraging area, it may be important for roosting.

## Clutter Sampling

My results suggest that the artificial clutter affected the foraging activity of bats. Prey availability between the treatment and the control did not differ, indicating that only the spatial complexity of the habitat type was manipulated. As expected, clutter-adapted bats foraged less within the clutter box than along the control edge. In contrast, the open-adapted

bats did not seem to be affected by this degree of spatial complexity. This is surprising, as I expected the open-adapted bats to be most dramatically influenced by the artificial clutter, due to their ecomorphological characteristics. That is, the faster, less manoeuvrable flight and relatively coarse resolution of echolocation calls of the open-adapted bats would limit them to more open habitat. I suspect that the clutter boxes were not large enough to properly sample the open-adapted bats, and that the bat detectors were actually monitoring open-adapted bats flying outside the clutter box. This may have occurred because, relative to clutter-adapted bats, open-adapted bats generally produce more intense echolocation calls of lower frequencies that travel greater distances (Griffin 1971).

#### Lake Sampling

Riparian areas appear to be primary foraging areas for bats, with much greater foraging rates observed there than in forest-harvested areas. My results suggest that the centre and edge of lakes are important foraging areas, particularly for clutter-adapted bats. Greater activity by clutter-adapted bats may reflect the prey availability associated with lakes. That is, smaller flying insects that emerge from the surface of the water may only be perceptible and available to the clutter-adapted bats, equipped with their slower, more manoeuvrable flight and finer resolution of echolocation calls.

#### CONCLUSIONS

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My results suggest that habitat use by foraging bats depends on the spatial complexity of a habitat type in combination with prey availability. The disturbance associated with forest harvesting appears to create preferred habitat for foraging bats, particularly for large bats that may be restricted to open habitat. My data suggest that edge and clear-cut habitats are preferred, and that forest habitat is not an important foraging area. However, the forest habitat may be important as a prey source for bats, as well as for potential roosting habitat. Furthermore, lake habitat, and most likely other riparian areas, appear to be primary foraging areas for bats, and need to be managed accordingly. Therefore, there must be balance between the creation of beneficial feeding areas along clear-cut edges, and the requirements for prey resources and suitable roosting sites, associated with forest habitat.

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