Effects of Timber Harvest on Bat Activity in Southeastern Alaska's Temperate Rainforests

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ABSTRACT

Five species of bats occur in southeastern Alaska's coniferous rainforests: *Myotis lucifugus*, *M. californicus*, *M. volans*, *M. keenii*, and *Lasionycteris noctivagans*. Over 42% of the high-volume timber in southeastern Alaska has been harvested, raising concern about wildlife habitat and conservation. We studied bat activity in old-growth forests, riparian areas, closed-canopy, second-growth forests, and clearcuts on Prince of Wales and Revillagigedo islands using ultrasonic bat detectors. Bats foraged in riparian areas, and activity patterns in this habitat differed during lactation and post-lactation. Bat calls detected in old-growth forests consisted primarily of commuting activity. Bats fed in clearcuts, but activity was low. Bat activity in second-growth was very low. Activity levels and nightly activity patterns make it clear that conservation of old-growth forests and riparian areas is essential for continued viability of the southeastern Alaska bat community. Diet and reproduction of *M. lucifugus* in these temperate rainforests differed from that reported at lower latitudes. Preliminary diet information for *M. keenii* and *M. volans* in southeastern Alaska is also presented. Over 300 caves have been surveyed in southeastern Alaska's 1,769 km^2 of karst terrain. Evidence of bats occupying these caves is widespread, and seasonality of that occupation is just beginning to be assessed. We provide evidence that neither clearcuts, nor second-growth forests provide habitat characteristics essential to most southeastern Alaska bats during the summer. This study also provides strong evidence that old-growth forests and riparian zones provide habitat characteristics needed by bats.

INTRODUCTION

Microchiropteran bats are long-lived nocturnal insectivores with low reproductive rates and non-cyclic populations (Findley 1993). These characteristics allow bats to achieve constant population levels in stable habitats, but may make them vulnerable when habitat is modified. Many bat populations have suffered decline, and some are threatened or endan-

gered (Tuttle 1979; Lowe et al. 1990; Speakman et al. 1991), due in part to habitat alteration (Lowe et al. 1990; Adam et al. 1994). The southeastern Alaska bat community consists of five species. *Myotis californicus*, *M. volans*, *M. keenii*, and *Lasionycteris noctivagans* reach the northern limit of their range in southeastern Alaska. *Myotis lucifugus*, the most commonly encountered bat species in southeastern Alaska, also occurs in more northerly parts of Alaska and Canada (Youngman 1975; Hall 1981; Parker et al. unpublished data).

Over 42% of the most productive forests (timber volume classes 6 and 7) in southeastern Alaska had been harvested by 1990 (United States Department of Agriculture 1991, 1993), and extensive harvesting continues. To determine whether southeastern Alaska forests are important bat habitat, we compared relative bat activity levels in high-volume, old-growth forests, riparian areas, clearcuts, and closed-canopy, second-growth forests. We also analyzed the nightly pattern of bat activity and relative feeding activity. Preliminary data were collected on bat diets, *M. lucifugus* reproduction, and seasonal bat occupation of caves.

METHODS

Study Area

This study was conducted in southeastern Alaska from 29 May through 28 August 1993. Southeastern Alaska is the wettest and coldest part of the north-temperate coniferous rainforest zone (Walter 1985). This ecosystem stretches from 54° to 60°N latitude, and includes the Alexander Archipelago and a narrow strip of mainland coast. The coastal mountain range and glacier fields isolate the region geographically and climatologically from nearby British Columbia and south-central Alaska (Figure 1).

Study sites were on northern, central, and southeastern Prince of Wales and western Revillagigedo islands at 55° to 56°N latitude (Figure 2). Prince of Wales, the third-largest island in the United States, covers 4557 km^2. Karst topography is well developed over much of northern and central Prince of Wales Island. This karst landscape has many caves and crevices, and contains some of the most productive forests on the island (Aley et al. 1993). Study sites were on harvested and unharvested areas of karst as well as non-carbonate lands (Table 1). Revillagigedo Island is approximately one-half the size of Prince of Wales Island and has little karst. Study sites on this island were on non-carbonate terrain. Heavy rains occur in all seasons throughout the study area. Annual precipitation varies from 4064 mm on western Revillagigedo Island to 2032 mm on northern Prince of Wales Island (Hartman and Johnson 1978).

Forest Habitats Monitored

Habitats investigated were (1) old-growth forests dominated by western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), and red cedar (*Thuja plicata*); (2) riparian areas (edge of streams or ponds 10–25 m wide, Table 1) within these forests; (3) closed-canopy, second-growth forests harvested 25–70 years ago; and (4) forests clearcut-harvested 5–17 years ago in which the canopy had not yet closed. Six sites in each of the four habitat types were monitored. The 24 study sites were all >16 ha and at elevations <250 m. Dominant overstorey (tree) and understorey (shrub

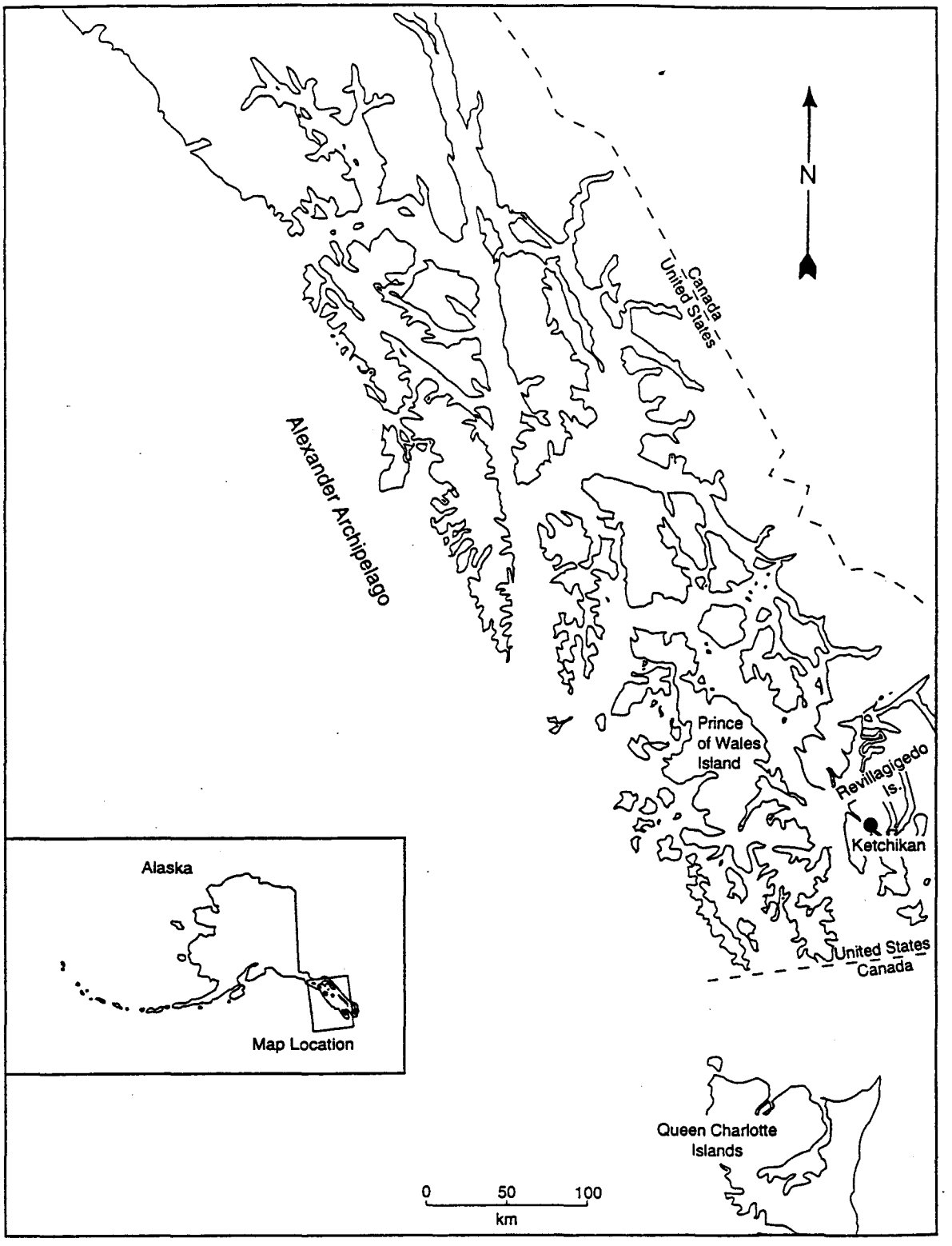

FIGURE 1 *Southeastern Alaska.*

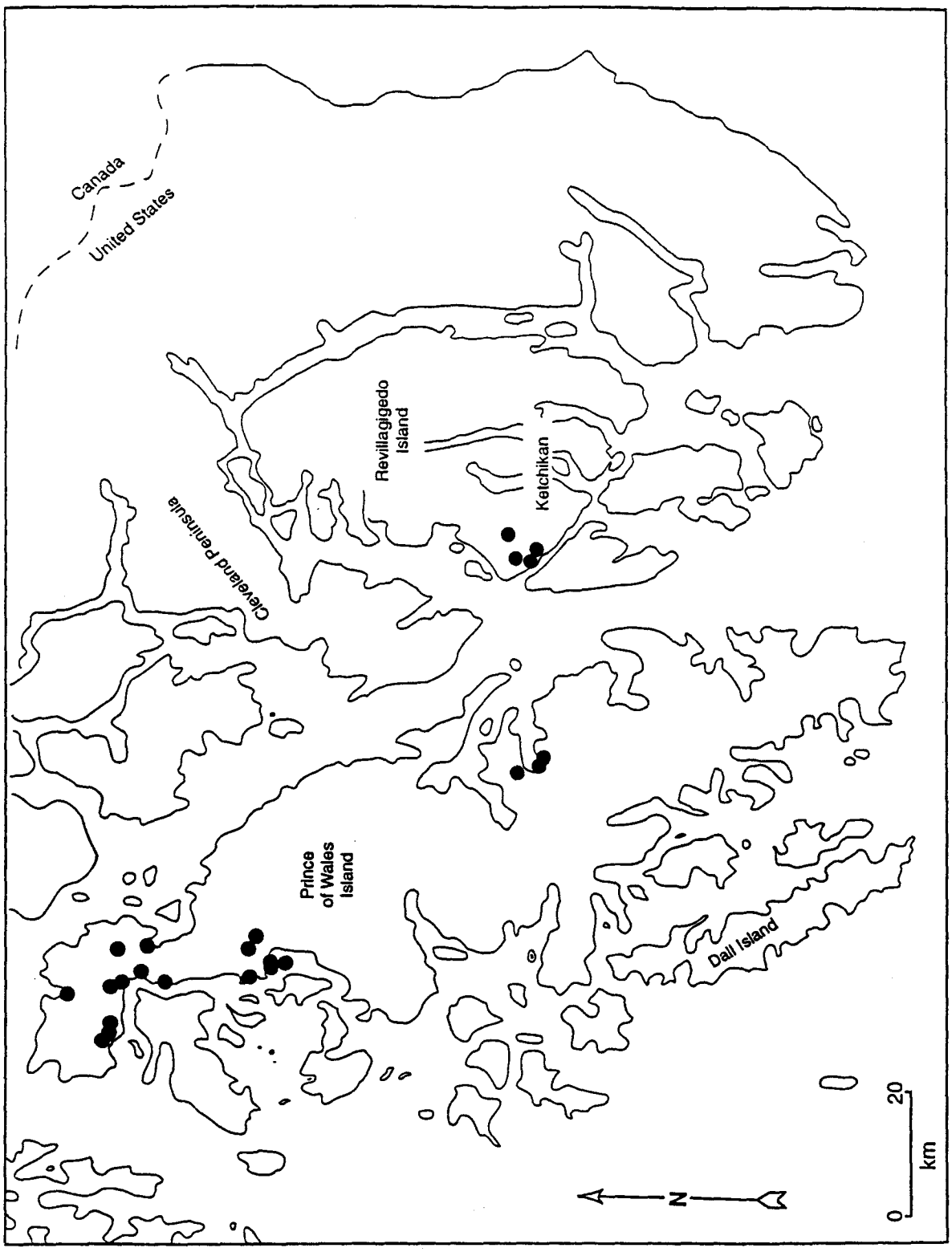

FIGURE 2 *Study area on Prince of Wales and Revillagigedo islands in southeastern Alaska.* ● *represent study sites.*

TABLE 1 *Vegetation characteristics and karst occurrence of 20 x 40 m plot at study sites*

Site name	Karst	Dominant overstorey species[1]	Dominant understorey species[1]	Canopy height[2]	Number trees[3]	Number snags[4]	Stream width	Stream grad
Riparian sites								
Red Creek	no	WH/SS	Vacc/DC	24 m	28	7	20 m	2%
Turn Creek	yes	WH/SS	Vacc	27 m	26	2	10 m	2%
108 Creek	no	WH/SS	Vacc/SC	34 m	7	6	18 m	2%
Yatuk Creek	yes	WH/SS	DC/SB	37 m	12	1	10 m	2%
Polk Creek	no	WH/RC	Vacc/SL	31 m	23	14	25 m	4%
Frog Pond	no	SP	CB	7 m	10	0	15 m	0%
Old-growth sites								
Calder	yes	WH/RC	Vacc/SF	31 m	34	9		
Beaver Falls	yes	WH/SS	Vacc/DC	33 m	33	5		
River's End	yes	WH	Vacc/DC	34 m	15	7		
Sarkar	no	WH	Vacc	34 m	18	2		
Polk	no	WH	Vacc/DC	31 m	28	7		
Perseverance	no	WH/RC	Vacc/SC	30 m	31	6		
Clear-cut sites								
Calder	yes	WH/SS[5]	Vacc	5 m	0	0		
Roaring Road	yes	WH[5]	Vacc/DC	2 m	0	0		
Naukati	yes	WH/SS[5]	Vacc	1 m	0	0		
Yatuk	no	WH[5]	Vacc	3 m	0	0		
Polk	no	WH[5]	Vacc	2 m	0	0		
Ketchikan	no	WH[5]	Vacc/SC	2 m	0	0		
Second-growth sites								
Calder	yes	WH/SS	Vacc	18 m	86	1		
Starlight	yes	WH/SS	Vacc/DC	10 m	37[6]	1		
Naukati-1	yes	WH/SS	Vacc	18 m	110	2		
Naukati-2	yes	WH/SS	Vacc	18 m	104	2		
Polk	no	WH/SS	Vacc/DC	17 m	52	0		
Pipeline	no	WH	Vacc/DC	12 m	60	1		

[1] WH = *Tsuga heterophylla* (western hemlock), SS = *Picea sitchensis* (Sitka spruce), RC = *Thuja plicata* (red cedar), SP = *Pinus contorta* (shore pine), Vacc = *Vaccinium alaskaense/ovalifolium* (blueberry species), DC = *Oplopanax horridum* (devil's club), SC = *Lysichitum americanum* (skunk cabbage), SL = *Gaultheria shallon* (salal), SF = *Polysticum munitum* (swordfern), SB = *Rubus spectabilis* (salmonberry), CB = *Empetrum nigrum* (crowberry).

[2] Average canopy height of overstorey trees in riparian, old-growth, and second growth. Average height of young trees in clearcuts.

[3] Number of trees ≥ 12 cm DBH (diameter at breast height).

[4] Number of dead trees ≥ 12 cm DBH and ≥ 2 m tall.

[5] Tree species before harvest.

[6] Site thinned in mid-1980s.

and herb) species at each study site (Table 1; DeMeo et al. 1992) were described. To ensure within-habitat uniformity, we estimated overstorey height with a clinometer and tape, and quantified trees and snags within a 20 × 40 m area at each site. Multiway analysis of variance determined that there were significant structural differences among the four habitat types ($p < 0.05$; Zar 1984). Tukey pairwise comparisons determined that average stand height, number of trees per plot, and number of snags per plot differed between habitats (Table 2; $p < 0.05$; Zar 1984). Sample size was too small to determine within-habitat differences between karst and non-karst sites.

Activity Levels and Types of Calls

To determine relative levels of bat activity among habitat types, echolocation calls were recorded with countdown-mode bat detectors and delay switches (Anabat II, Titley Electronics, Ballina, N.S.W., Australia) attached to voice-activated, cassette tape-recorders (Radio Shack Realistic Minisette 20). A single bat call was defined as ≥ 2 ultrasonic pulses (Griffin 1958) detected from the time the bat detector began recording calls until the calls were no longer audible. The time of each call was recorded automatically. The electronic equipment was placed in a plastic box with a hole for the microphone and a 3-cm roof to shelter the microphone from rain. A light sensor turned the system on at dusk and off at dawn. One bat detector was placed in each site at least 90 m inside the habitat and approximately 2 m above the ground. To reduce the effect of weather, all habitat types were monitored every night. All 24 sites were monitored ultrasonically for 1 to 9 nights (average 4.6).

Bat calls were transcribed from the recordings and grouped in 5-minute intervals. Anabat II Bat Call Analysis software version 1.1 (Titley Electronics, Ballina, N.S.W., Australia) was used to display call sonagrams to determine whether questionable sounds were bat calls or extraneous noise (e.g., raindrops). We could not unequivocally differentiate species of *Myotis* by their calls because the vespertilionid species inhabiting southeastern Alaska are difficult to differentiate by their call characteristics (Thomas et al. 1987; Thomas 1988). A feeding buzz was defined as an increased pulse repetition rate that blended the calls together into a buzz (Griffin 1958). To test for differences in the proportion of nights with bat activity and the proportion of calls containing feeding buzzes, we used χ^2 tests (Zar 1984). Because bat calls were not normally distributed and variances were not equal, Kruskal-Wallis one-way analysis of variance was used to compare average calls per night among habitat types.

TABLE 2 *Tukey pairwise comparisons of habitat characteristic means ($p \leq 0.05$)*

Habitat type	Stand height	Number of trees	Number of snags
Riparian	A	B	AB
Old growth	A	B	A
Clearcut	B	C	CB
Second growth	C	A	C

Means with the same letter are not significantly different.

Activity Patterns

To test whether nightly activity patterns differed between habitat types or temporally, we compared nightly patterns of call activity in the periods 14–21 July and 17–28 August. Only old-growth and riparian sites had adequate activity for comparison. To remove the bias of fewer calls at the end of the night due to rain noise running the tape out or battery failure, we calculated a weighted average of calls-per-5-minute-interval in which equipment was working. To remove autocorrelation, we used a moving average of 5 intervals. Time from sunset to sunrise increased from 7 hours 6 minutes to 9 hours 58 minutes between 14 July and 28 August. Length of twilight decreased from 48 minutes (13% of the night) to 18 minutes (3% of the night). Therefore, we compared intervals beginning 30 minutes before sunset, rather than using clock time. Activity that occurred later than 7 hours 9 minutes after sunset (i.e., sunrise on 14 July) was excluded from comparison. Resulting patterns were compared using Kolmogorov-Smirnov goodness of fit tests for cumulative data (Zar 1984). Because of the small data set, we tested only whether overall patterns differed, and did not statistically compare portions of the night.

RESULTS

Activity Levels and Call Type

One-hundred and fifteen nights of sampling yielded 2716 bat calls. There were 2508 bat calls detected in riparian habitat during 31 nights sampled; 150 calls in old growth during 25 nights; one call in second growth during 30 nights; and 57 calls in clearcuts during 29 nights (Table 3). In addition to calls listed above, bats were detected on two additional nights in riparian sites, but the number of calls could not be determined. These nights were only used to compare the proportion of nights with bat activity. Proportion of nights with bat activity (≥ 1 call per night) differed significantly between the four habitats ($\chi^2 = 33.04$, $p \leq 0.05$). Pairwise comparisons showed no significant difference in number of nights with activity in riparian versus old growth ($\chi^2 = 0.71$, $p \leq 0.05$). There were significantly more nights with activity in old growth than in clearcuts ($\chi^2 = 6.29$, $p \leq 0.05$), and in clearcuts than second growth ($\chi^2 = 5.70$, $p \leq 0.05$).

TABLE 3 *Bat activity in forest habitats*

Habitat type	Total number of calls	Number of nights sampled	Average calls per night[a]	Percentage of nights with bat activity[a]	Percentage of calls with feeding buzz[a]
Riparian	2508	31 + 2[b]	81 A	97 A	15 A
Old growth	150	25	6 B	76 B	4 B
Clearcuts	57	29	2 B	28 C	10 B
Second growth	1	30	0.03 C	3 D	0
Total	2716	115			

[a] Items with the same letter are not significantly different ($p \leq 0.05$).

[b] 31 nights were used to calculate percentage of total calls and average calls per night, 33 nights were used to calculate percentage nights with bat activity. See text for explanation.

Average number of calls per night among the four habitats was significantly different ($H = 68.27$, $p \leq 0.001$). Multiple comparisons showed significant differences between riparian and old growth ($H = 3.40$, $p \leq 0.05$), old growth and second growth ($H = 3.82$, $p \leq 0.05$). Differences between average calls per night in old growth and clearcuts were not significant ($H = 2.48$, $p \leq 0.05$). However, 47 of the 57 calls in clearcuts occurred during the night of 5 July. There was no significant difference in average calls per night between clearcuts and second growth ($H = 1.40$, $p \leq 0.05$). In riparian sites, a sample of 731 calls revealed that 110 contained feeding buzzes, while in old growth 6 of 150 calls contained feeding buzzes. In clearcuts, 6 of 57 calls contained feeding buzzes; 5 of these were among the 47 calls detected on 5 July. The single call in second growth did not contain a feeding buzz. There was a significant difference in proportion of calls that contained feeding buzzes among riparian, old growth, and clearcut habitats ($\chi^2 = 11.97$, $p \leq 0.05$). Pairwise comparisons showed significant differences between riparian and old growth ($\chi^2 = 11.57$, $p \leq 0.05$), but not between clearcuts and riparian ($\chi^2 = 0.734$, $p \leq 0.05$), or between clearcuts and old growth ($\chi^2 = 3.05$, $p \leq 0.05$).

Activity Patterns

Calls were not detected before sunset or after sunrise in any habitat during the study period (Figure 3). Activity patterns differed significantly between old-growth and riparian habitats in July ($df = 88$, $p \leq 0.001$, $D = 0.205$); in August between old-growth and riparian habitats ($df = 126$, $p \leq 0.001$, $D = 0.172$); and in riparian habitat between July and August ($df = 88$, $p \leq 0.001$, $D = 0.205$). There was no significant difference between July and August activity patterns in old growth ($df = 94$, $p > 0.05$, $D = 0.138$). Both July and August activity in riparian areas began 15–20 minutes after sunset. In July there were two additional activity peaks within 4 hours of sunset, and almost no activity during the next 3 hours before sunrise. In August, activity was low throughout the remainder of the night, even though the night was longer and twilight was shorter.

DISCUSSION

Riparian Areas

Riparian habitat had the highest proportion of nights in which bats were detected, the highest number of bat calls per night, and the highest proportion of calls containing feeding buzzes. Among the four habitats sampled, riparian areas were the most important foraging sites for bats. The importance of riparian areas as feeding habitat has been frequently noted at lower latitudes and in drier climates (Buchler 1976; Fenton and Bell 1979; Bell 1980; Nagorsen and Brigham 1993). *Myotis lucifugus*, the most commonly encountered species in southeastern Alaska (Parker et al. unpublished data), tends to circle when foraging (Fenton and Bell 1979; Fenton et al. 1980). The higher number of bats detected per night may have been influenced by individual bats being detected multiple times as they foraged. Nevertheless, the higher proportion of nights that bats were detected in riparian habitat, and the high proportion of calls containing feeding buzzes in these sites support the conclusion that riparian areas are important bat habitat.

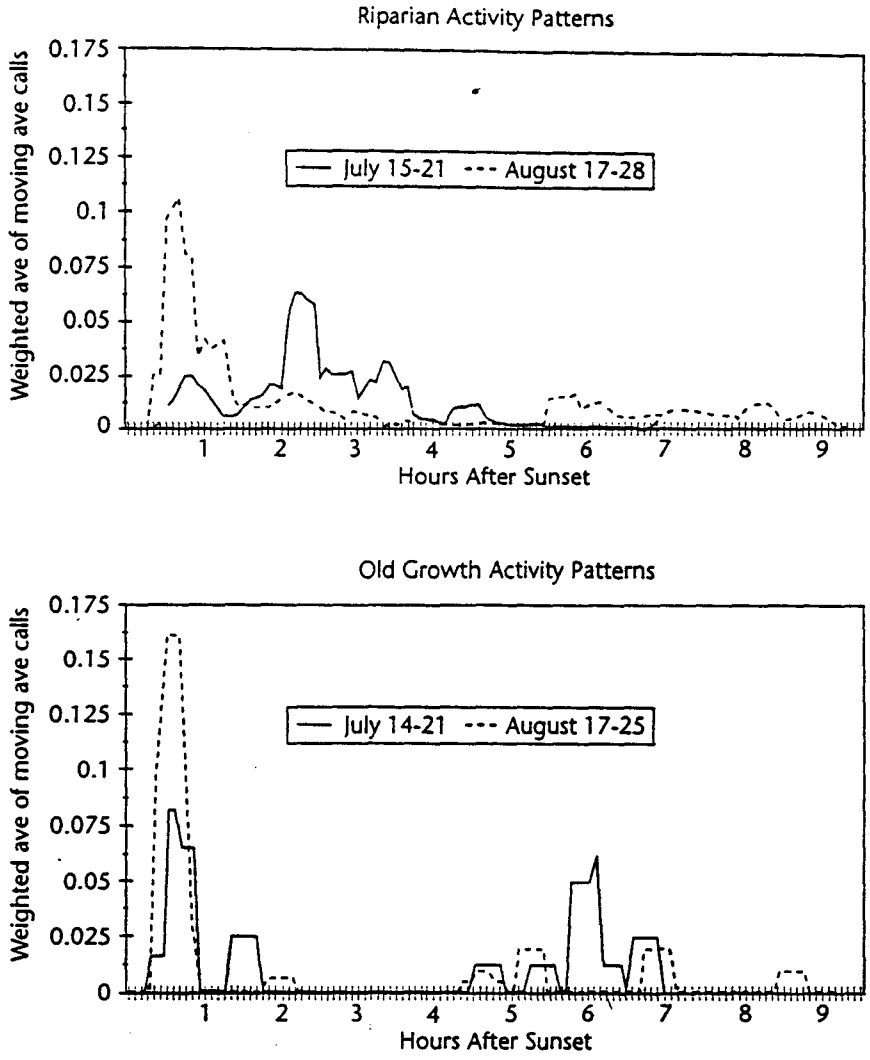

FIGURE 3 *Activity patterns during 14–21 July and 17–28 August in riparian and old-growth sites.*

The temporal change in activity patterns in riparian areas likely reflects seasonal changes in energy needs at this high latitude. We suggest that the prolonged foraging activity in July is in response to the high energy demand of lactation and the subsequent need to forage longer. This corroborates other studies that found that female *M. lucifugus* forage up to 4 hours per night during late pregnancy and lactation (Kurta et al. 1989), and forage several times per night, returning to the maternity roost to nurse their young between foraging bouts (Anthony and Kunz 1977; Anthony et al. 1981). By mid-August, females no longer have the high-energy demand of lactation (Kurta et al. 1987), and can meet energy needs in a shorter period of time (Anthony and Kunz 1977). This is reflected by the August activity pattern, in which most activity occurred within 2 hours of sunset. Insect availability is low during the latter part of the night (Anthony and Kunz 1977; Barclay 1991), and probably makes foraging less efficient than conserving energy (Pulliam 1981) by roosting. Foraging juveniles may account for the low-activity level during the remaining

8 hours before sunrise in August. Juveniles are less adept at capturing insects, and must forage longer to meet energy needs (Anthony and Kunz 1977). A similar change in foraging patterns was noted for *Pipistrellus pipistrellus* at 57°N latitude in Scotland. During lactation these bats foraged just after sunset and again prior to sunrise. During pregnancy and post-lactation they foraged only once, immediately following sunset (Swift 1980). In contrast to our study, Anthony et al. (1981) found that *M. lucifugus* in New Hampshire had a bi-modal pattern of foraging activity throughout the summer. Differences in study methods may be responsible for differences observed between this study and *M. lucifugus* in New Hampshire. We monitored echolocation calls in riparian habitat, whereas Anthony et al. (1981) monitored bats leaving and entering night roosts.

Old-Growth Forests

Old-growth was the habitat with the second-highest bat activity. Even though old-growth sites had fewer average calls per night, calls were heard during 76% of nights monitored. This regular occurrence of bats suggests that it is important for summer roosts. Southeastern Alaska's temperate rainforests contain abundant live trees, snags, and fallen logs in a variety of sizes (Alaback 1991). Such structural diversity provides suitable sites for cavity-roosting species (Bunnell and Allaye-Chan 1984), such as bats (Barclay and Cash 1985; Christy and West 1993). Use of old-growth forests by bats for roosting and foraging has been documented in British Columbia, Washington, and Oregon (Barclay and Cash 1985; Lunde and Harestad 1986; Thomas 1988; Christy and West 1993). Bat roosts and foraging sites are likely to occur throughout old-growth forests, dispersing bats and decreasing the likelihood of a bat passing by an ultrasonic detector placed randomly in the forest. In addition, because bats in old-growth sites were primarily commuting, they were not likely to pass the detector more than once. The six calls with feeding buzzes in old growth indicate that foraging also occurred in old growth. It is likely that all bat species in southeastern Alaska forage in old-growth forests (Saunders and Barclay 1992; Nagorsen and Brigham 1993; van Zyll de Jong and Nagorsen 1994), especially *M. keenii* (Parker and Cook, in review). Nightly activity patterns in old growth remained the same in July and August. This predominantly commuting activity was highest immediately following sunset when bats left their roosts to travel to foraging sites. A few bats were detected at different intervals throughout the rest of the night, and may have been bats returning to day roosts.

Old-growth forests in southeastern Alaska may be important to bats primarily for roosting sites. However, too little is known about the ecology of bats in these temperate rainforests to be sure that they are not equally important as foraging areas for species, such as *M. keenii* (Parker and Cook, in review). Availability of roost structure is thought to be an important factor limiting bat distribution and abundance in temperate climates (Humphrey 1975; Kunz 1982). In other portions of their range, *M. lucifugus*, *M. volans*, *M. californicus*, *M. keenii*, and *L. noctivagans* roost under loose bark, in snags, and hollow trees (Barclay and Cash 1985; Thomas 1988; Christy and West 1993). In addition, extensive karst formations in southeastern Alaska (Buddington and Chapin 1929; Aley et al. 1993; Baichtal, 1995) provide numerous caves and crevices where hibernating bats have been observed (Parker et al. unpublished data).

Clear-cut Forests

The smaller proportion of nights in which bats were detected in clearcuts rather than in old growth indicates that bat activity in old growth was more consistent. This is likely due to the lack of roost structure in clearcuts. Clear-cut harvest of timber eliminates snags, decaying trees, and large trees with loose bark (Cline et al. 1980), thereby eliminating roost sites.

Insectivorous bats exploit patches of insects (Belwood and Fenton 1976; Bell 1980), and this is apparently what at least one bat was doing in the clearcut that showed unusually high bat activity on 5 July. Activity on that night also influenced the lack of statistical significance in the average calls per night between clearcuts and old-growth or riparian habitats. Clearcuts in southeastern Alaska may be used occasionally by *L. noctivagans* and *M. volans*, which sometimes forage in open areas (Fenton and Bell 1979; Nagorsen and Brigham 1993).

Second-Growth Forests

The high density of even-sized, closely spaced trees, and the lack of snags and decaying trees in second growth (Alaback 1984a; Bunnell and Allaye-Chan 1984) are likely reasons for the low activity of bats in this habitat. In southeastern Alaska, old-growth characteristics, including the structural diversity needed for roosts, begin to develop 150–200 years after harvest (Alaback 1984b). It is possible that bats commonly foraged above the second-growth canopy and were not detected because the dense canopy blocked echolocation calls. However, the single echolocation call recorded in second growth indicates that it is possible to detect calls in this habitat. More calls should have been recorded if bats foraged above the second-growth canopy. In a similar study in the Pacific Northwest, bats were detected three to ten times less often in second-growth than in old-growth forests, even when bat detectors were placed in the tree canopy as well as on the ground (Thomas 1988). Our study indicates that little bat activity occurs in second-growth forests of southeastern Alaska.

Ecology of *Myotis lucifugus*

Reproduction in *M. lucifugus* also appears to differ between southeastern Alaska and lower latitudes. At lower latitudes, in areas of high summer rainfall and low ambient temperature, *M. lucifugus* has a low female:male ratio, and females are non-reproductive (Thomas 1988; Barclay 1991). Inclement weather may not allow sufficient time during the night for females to meet energy demands of pregnancy and lactation (Thomas 1988; Barclay 1991; Grindal et al. 1992). In southeastern Alaska, however, the female:male ratio is equal, and reproductive females have been captured (Parker et al. unpublished data). This suggests that female *M. lucifugus* are able to meet the energy demands of pregnancy and lactation in southeastern Alaska rainforests, even though prolonged rainstorms are common. Changes in activity patterns between lactation and post-lactation support this conclusion. Consumption of over 15% non-volant prey, such as spiders (Parker, unpublished data; Whitaker and Lawhead 1992), may enable these bats to maintain a positive energy balance.

CONCLUSIONS

Federal law in the United States requires public land managers to inventory and maintain viable populations of wildlife affected by land-management practices, such as timber harvesting (United States Congress 1976). Our study suggests that old-growth forests and riparian areas provide roosting and foraging habitat for the five bat species in southeastern Alaska. Extensive past and future harvesting in southeastern Alaska (United States Department of Agriculture 1991, 1993) suggests a significant impact on these species. Our data also indicate that clearcuts are not important bat habitat, perhaps because clearcuts do not provide roosting structure. However, bats occasionally fed on insect swarms in clearcuts. Closed-canopy second growth is not used by bats in southeastern Alaska. Old-growth characteristics that provide suitable roost sites for bats do not develop until at least 150 years after harvesting. Current plans for the Tongass National Forest project a 150-year harvest rotation (United States Department of Agriculture 1991). Planning and environmental assessment processes for public lands should include this information when considering the effects of land-management practices.

Southeastern Alaska is unique among high-latitude archipelagos because of its large number and high diversity of caves (Aley et al. 1993; Baichtal, 1995). Over 1,769 km^2 of southeastern Alaska's 26,305 km^2 Tongass National Forest are on karst terrain (United States Department of Agriculture, in press). Caves and crevices are also important bat habitat (Hill and Smith 1984). Personal observations (Parker and Cook) suggest that bats occupy caves during cold spells in the winter, but leave these caves during warmer spells. Guano and skeletal remains have been observed in several caves. However, during eight summers of intensive mapping and exploration of more than 340 significant caves, no bats have been observed (Lewis and Allred, unpublished data). Future studies should examine seasonal changes in roost selection to determine when bats in southeastern Alaska occupy forest and cave roosts. Studies should also assess what aspects of cave morphology create microclimates suitable for hibernating bats. Because some of the most productive forests in southeastern Alaska are on karst (Baichtal, 1995), this component of southeastern Alaska's rainforest ecosystem should be especially important bat habitat, providing forest and cave roosts, as well as foraging habitat. Documentation of winter activity patterns and foraging strategies in relation to weather patterns and habitat type will be important in determining the effects of timber harvesting on bats.

Our study provides evidence that the ecology of *M. lucifugus* in southeastern Alaska cannot be extrapolated from studies of this species at lower latitudes. Reproduction appears to differ between *M. lucifugus* in southeastern Alaska and conspecifics at lower latitudes. Ecology of *M. volans* and *M. keenii*, *M. californicus*, and *Lasionycteris noctivagans* in southeastern Alaska has not been established because no data are available for these species (Parker et al., unpublished data). Foraging strategies, prey availability, and reproductive success of these species should be assessed in southeastern Alaska.

Although questions remain about how habitat modification in south-

eastern Alaska affects bat populations, this study strongly suggests that present levels of timber harvesting will have a detrimental effect on these bat populations. We provide strong evidence that neither clearcuts, nor second-growth forests provide habitat characteristics essential to most southeastern Alaska bats during the summer. We also provide evidence that unharvested, old-growth forests and riparian zones provide habitat characteristics essential to bats.

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