

Distributional Limits of Bats in Alaska

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ABSTRACT. Bats in temperate regions are relatively well studied, yet little research has focused on the northern limit of their distribution. We document the northwestern extent of bats in North America using museum holdings, literature records, and field research in Alaska. Six bat species are confirmed from Alaska: *Myotis lucifugus*, *M. keenii*, *M. californicus*, *M. volans*, *Lasionycteris noctivagans*, and *Eptesicus fuscus*. *M. lucifugus* occurs throughout much of Alaska south of the Arctic Circle, whereas four other species occur only in Southeast Alaska. Climate, roost availability, extent of forested habitat, geographic barriers, length of night, and prey abundance appear to influence the distribution of bats in Alaska, although the relative contribution of these factors is unknown.

Key words: Alaska, latitude, bats, distribution, limiting factors, *Myotis*, *Lasionycteris*, *Eptesicus*

RÉSUMÉ. Si, dans les régions tempérées, les chauves-souris ont fait l'objet d'études relativement approfondies, on a par contre mené peu de recherches sur la limite septentrionale de leur répartition. Cet article décrit l'extension nord-ouest de l'aire des chauves-souris en Amérique du Nord en faisant appel à des pièces muséologiques, des documents comportant des relevés, et des recherches sur le terrain en Alaska. On confirme que six espèces de chauves-souris se retrouvent en Alaska: *Myotis lucifugus*, *M. keenii*, *M. californicus*, *M. volans*, *Lasionycteris noctivagans* et *Eptesicus fuscus*. *M. lucifugus* est répandue presque partout en Alaska au sud du cercle polaire, tandis que quatre autres espèces ne se retrouvent que dans le sud-est de l'Alaska. Il semble que le climat, la disponibilité des sites de reproduction, l'étendue de l'habitat forestier, les barrières géographiques, la longueur de la nuit et l'abondance des proies influencent la distribution des chauves-souris en Alaska, bien qu'on ne connaisse pas la contribution relative de ces facteurs.

Mots clés: Alaska, latitude, chauves-souris, distribution, facteurs limitants, *Myotis*, *Lasionycteris*, *Eptesicus*

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INTRODUCTION

Alaska encompasses approximately 1.5 million km² of northwestern North America, an area 15% the size of Canada and 20% the size of the contiguous 48 United States. Across this broad expanse, climatic differences create vegetation zones ranging from coniferous rainforests in the Alexander Archipelago of Southeast Alaska to boreal forests in central Alaska and coastal tundra in western and northern Alaska (Viereck et al., 1992). The high latitude, large area, and variety of habitats in Alaska provide a unique opportunity to study distribution and latitudinal gradients of temperate species at the northern limits of their ranges.

There is abundant literature regarding the distribution and ecology of bats in North America (Barbour and Davis, 1969; Humphrey and Cope, 1976; Hall, 1981; van Zyll de Jong, 1985; Nagorsen and Brigham, 1993). Although it has been known for over 100 years that bats occur in Alaska (Turner, 1886), no comprehensive compilation of bat specimen records has been published. Most species were documented by a few specimens collected by early naturalists (True, 1886; Heller,

1909, 1910; Swarth, 1911; Grinnell, 1918; Miller and Allen, 1928), representing incidental captures rather than a systematic search for bats. Manville and Young (1965) summarized the available data for all bat species in Alaska in a few paragraphs, but did not document the specimen records portrayed on their range map. Hall (1981) provided the best summary prior to our effort. In this paper, we describe the occurrence and distributional limits of bats in Alaska. We provide a foundation for future research by clarifying species distribution patterns and identifying factors that may influence bats in Alaska.

METHODS

We investigated the occurrence of bats in Alaska through a review of published and unpublished literature, verification of museum specimens, and recent field studies we conducted in Southeast Alaska during 1990–95. Southeast Alaska extends from 54°30' to about 60°N, and includes thousands of islands in the Alexander Archipelago and a narrow strip of

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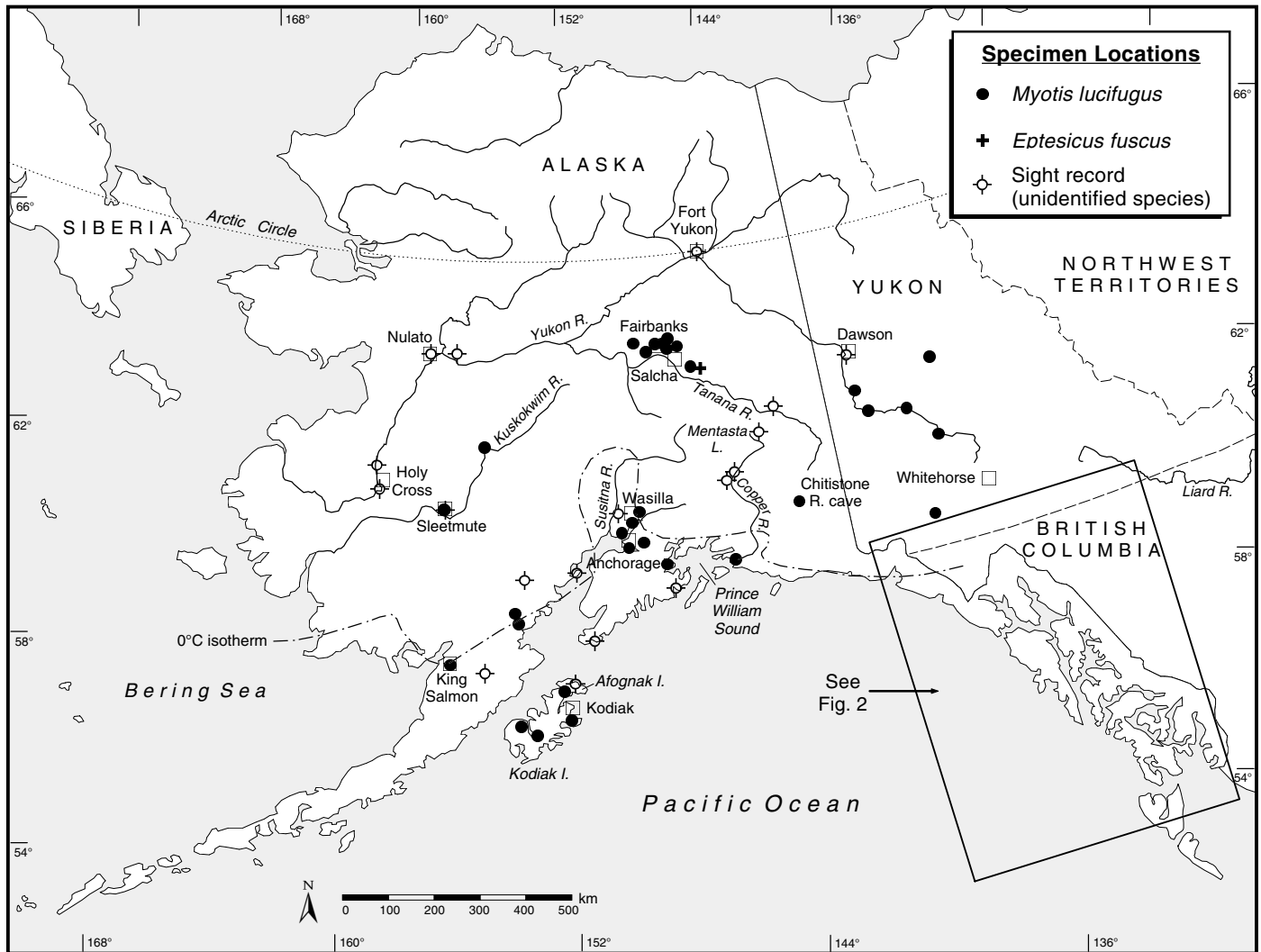


FIG. 1. Location of bat specimens collected in Alaska. Isotherm depicts approximate location where mean annual surface temperature reaches freezing (interpolated from Hartman and Johnson, 1984).

rugged mainland coast (Figs. 1 and 2). The region is isolated geographically and climatologically from south-central Alaska and interior British Columbia by extensive ice fields of the St. Elias and Coast mountains. Our methods included mist netting and collecting from roosts (MacDonald and Cook, 1996; Parker, 1996; Parker and Cook, 1996). We also recorded 2716 echolocation calls in Southeast Alaska in 1993 (Parker et al., 1996). Many specimens collected prior to 1990 by other workers were shot. In total, 195 bat specimens are archived at the University of Alaska Museum. Twelve of 24 other North American museums that we contacted hold a total of 101 bat specimens from Alaska (see Appendix). We examined all specimens and confirmed identification using external and cranial characteristics (van Zyll de Jong, 1979, 1985; van Zyll de Jong and Nagorsen, 1994). Taxonomy follows Koopman (1993).

Maternity colonies (groups of female bats with young) were located to evaluate the extent of bat reproduction in Alaska. Reproductive status of female specimens is also reported. The sex ratio of *M. lucifugus* in summer was

compared with that recorded on the western slopes of the Cascade Mountains in Oregon (Thomas, 1988) by counting male and female *M. lucifugus* captured in Southeast Alaska between June and August in 1991–94, the only region and time period for which adequate data were available. The sex ratio was tested using a χ^2 test with an alpha level of 0.05.

RESULTS

All Alaska specimens, associated place-names, and corresponding latitudes and longitudes are listed in the Appendix. Figures 1 and 2 depict all specimens recorded in Alaska, selected place-names, and nearby Canadian specimen records. Museum acronyms follow Yates et al. (1987) (see Appendix).

Myotis lucifugus (Le Conte, 1831), Little Brown Bat

M. lucifugus is the most common and widely distributed bat in Alaska. We examined 279 specimens of *M. lucifugus*

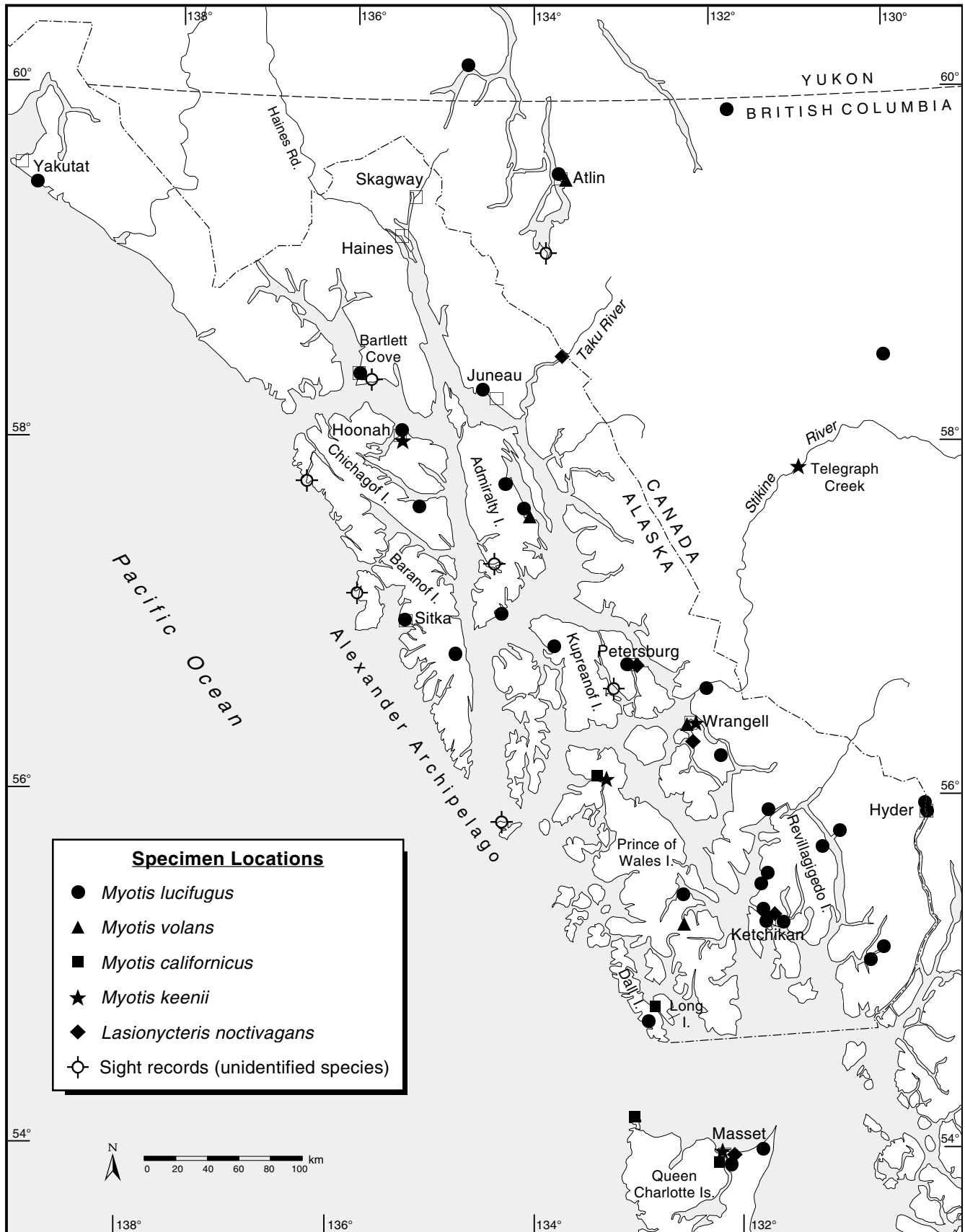


FIG. 2. Location of bat specimens collected in Southeast Alaska and neighboring areas of Canada.

from 54 locations, about 94% of all specimens from Alaska. This is the only species of *Myotis* collected north of 59°N latitude. Our methods of mistnetting and collecting from maternity colonies may bias captures toward *M. lucifugus*; thus, this species may not dominate the fauna in Southeast Alaska to the extent suggested by the specimen data. Historic collection efforts also have been sporadic and in widely separated locations, so our results probably do not fully reflect the regional abundance or range limits of this species. Nonetheless, our efforts document known range limits and seasons of occurrence.

The northernmost specimens of *M. lucifugus* are from the vicinity of Fairbanks, and the westernmost from near Sleetmute. The southernmost specimen is from Dall Island in Southeast Alaska. Most *M. lucifugus* were collected between 1 June and 31 August; exceptions are one female collected near Fairbanks on 26 May 1948 (UMDZ); four females and one male collected on Kodiak Island on 12 February 1883 (USNM); three females and one male collected at Loring, 20 km north of Ketchikan, between 17 and 22 September 1895 (USNM); and one male and one unsexed individual collected at Ketchikan in October 1909 (USNM).

In Southeast Alaska, 36 female and 41 male *M. lucifugus* were collected between June and August 1991–94; the sex ratio was not significantly different from 1:1 (χ^2 , $p \leq 0.05$). Data on reproductive status were available for 15 of these females: two pregnant females were collected on 13 June 1993, nine lactating individuals were collected between 15 June and 7 August, and four females that were neither pregnant nor lactating were collected between 28 June and 19 August. On 11 August 1993, a juvenile male was collected on Prince of Wales Island, suggesting that young in Southeast Alaska are independent by mid-August. In addition, 34 females were collected from a maternity colony in a house attic at Hyder on 10 June 1990. Of these, 28 were pregnant and 5 were not pregnant or lactating; reproductive data was not available for the remaining individual. Maternity colonies have also been located in buildings at Salcha (Whitaker and Lawhead, 1992), near Mentasta Lake, between Wasilla and Anchorage (J. Hughes, pers. comm. 1990), and at Bartlett Cove, Hoonah, Loring, and Ketchikan.

In addition to documented specimens, unidentified bats have been reported from a variety of locations in Alaska. Judging from the distribution of specimen records, it is reasonable to assume that bats sighted in central Alaska are *M. lucifugus*. The two northernmost records of *M. lucifugus* depicted by Hall (1981) are from Fort Yukon and Nulato; Turner (1886:205) reported that an “unidentified species of bat was reputed to inhabit these locations in summer.” Bats have been observed along the lower Yukon River near Holy Cross in summer, relatively far from potential roost sites in buildings (P. Bente, pers. comm. 1996). Mossman and Clark (1958) saw flying bats, presumed to be *M. lucifugus*, on Afognak Island in March 1954 and November 1956.

M. lucifugus occurs throughout the southern half of Yukon Territory, where at least 61 specimens have been collected in 11 locations. Bats assumed to be *M. lucifugus* have been

reported as far north as Dawson, Yukon Territory (Youngman, 1975). The species also has been reported at Hay River (60°52'N, 115°44'W) in the Northwest Territories and throughout British Columbia (van Zyll de Jong, 1985; Nagorsen and Brigham, 1993; Wilkinson et al., 1995).

Myotis volans (H. Allen, 1866), Long-legged Bat

Five specimens of *M. volans* have been collected in Alaska, all from the Alexander Archipelago (Fig. 2). A male (MVZ 186) was collected on 9 June 1907 on Admiralty Island (Heller, 1909). The specimen was originally misidentified as *M. lucifugus alascensis*, an error that was corrected by Grinnell (1918). On 29 July 1991, one lactating female (Alaska Department of Fish and Game collection) and two unsexed individuals (UAM 19756 and 19757) were collected in Wrangell (West, 1993). The fifth specimen (UAM 24822) was a female collected on 19 July 1993 on Prince of Wales Island. *M. volans* has been collected widely in British Columbia, where the northernmost record is from Atlin (Cowan and Guiguet, 1960).

Myotis keenii (Merriam, 1895), Keen's Long-eared Bat

The occurrence of *M. keenii* in Southeast Alaska has been substantiated by three specimens (Fig. 2; Parker and Cook, 1996). The first (USNM 187394, unsexed; Miller and Allen, 1928) was collected on 9 June 1887 at Wrangell. Like the first specimen of *M. volans*, it was initially misidentified as *M. lucifugus alascensis* (Miller, 1897) and later corrected by Grinnell (1918). A male *M. keenii* (UAM 23338) was captured on 20 July 1993 on northern Prince of Wales Island, approximately 65 km SW of Wrangell. The third specimen (UAM 29831), also a male, was collected on 11 July 1994 from a maternity roost of *M. lucifugus* at Hoonah, approximately 160 km N of the Wrangell specimen (Fig. 2; Parker and Cook, 1996).

M. keenii was once thought to be conspecific with *M. septentrionalis* but is now considered a distinct species (van Zyll de Jong, 1979). These two species also are difficult to distinguish from *M. evotis*, which is sympatric with *M. keenii* in British Columbia and Washington. The few locality records for *M. keenii* are restricted to coastal forests from Washington to Southeast Alaska (Nagorsen and Brigham, 1993; van Zyll de Jong and Nagorsen, 1994). The type locality for *M. keenii* is Masset, in the Queen Charlotte Islands of British Columbia. In British Columbia this species has been collected as far north as Telegraph Creek (USNM 209856; van Zyll de Jong, 1985).

Myotis californicus (Audubon and Bachman, 1842), California Bat

M. californicus has been collected only in Southeast Alaska: from Long Island, off the southwestern coast of Prince of Wales Island (two mummified specimens, Grinnell, 1918), and from El Capitan Cave on Prince of Wales Island (two

skeletons and one live bat, UAM). The only live *M. californicus* found (UAM 20498) was a hibernating female collected in February 1992 in El Capitan Cave. The nearest specimens in British Columbia are from the Queen Charlotte Islands at Masset (van Zyll de Jong, 1985). *M. californicus* has been captured as far north as the Liard River drainage (59°N, 126°W) in British Columbia (Wilkinson et al., 1995).

Lasionycteris noctivagans (Le Conte, 1831), Silver-haired Bat

Four female *L. noctivagans* have been collected, all in Southeast Alaska during winter (Fig. 2). The first (AMNH 213141, juvenile) was hibernating in a boat shed on the Taku River in November 1964 (Barbour and Davis, 1969). The second (UAM 20768) was found dead in a woodpile at Wrangell during February 1992. The third specimen (UAM 30100) was also found dead, clinging to the side of a house in Petersburg, on 1 January 1995; and the fourth (UAM 30099) was found alive in a house entryway in Ketchikan on 5 January 1995. These last two specimens were collected when the daytime temperature was about -7°C.

L. noctivagans is a migratory, tree-dwelling species (Barbour and Davis, 1969; van Zyll de Jong, 1985) that occurs throughout the southern part of Canada and most of the United States (Hall, 1981; van Zyll de Jong, 1985). Although the species has been reported as far north as Prince William Sound in Alaska (Manville and Young, 1965), we were unable to locate specimens or other data to substantiate that report. *L. noctivagans* has been collected in British Columbia on the Queen Charlotte Islands at Masset and Skidegate (Nagorsen and Brigham, 1993) and has been captured as far north as the Liard River drainage on the mainland (Wilkinson et al., 1995).

Eptesicus fuscus (Palisot de Beauvois, 1796), Big Brown Bat

E. fuscus has been collected only once in Alaska, near Big Delta in the interior of the state north of the Alaska Range (Appendix; Fig. 1). William D. Berry collected an adult female (UMDZ 111095) from a cabin at the mouth of Shaw Creek on 5 September 1955 (Reeder, 1965). The nearest specimen record of this species in Canada is from Pine Lake in northern Alberta (52°N, 113°W; Hall, 1981; van Zyll de Jong, 1985), 1600 km from Shaw Creek. Echolocation calls of *E. fuscus* have been recorded in the Liard River watershed of British Columbia (59°N, 126°W; Wilkinson et al., 1995), 1100 km from Shaw Creek. Because the Shaw Creek specimen was found approximately midway between the range of *E. fuscus* in Canada and *E. nilssoni* in Siberia, we also examined the specimen with regard to the characteristics of *E. nilssoni* (Ognev, 1962) and verified its identity as *E. fuscus*. The report by Manville and Young (1965) that *E. fuscus* occurs in Southeast Alaska could not be verified by specimens, and no calls of this species were recorded there in our echolocation surveys.

DISCUSSION

As for many organisms, species richness of bats decreases with increasing latitude (Findley, 1993). However, no single factor explains this relationship (Huston, 1994). Within Alaska, bats exhibit this latitudinal gradient and offer a good opportunity to examine potential causal factors. Below, we synthesize current knowledge of bat distribution in Alaska and outline some factors that may influence the relationship between latitude and species richness.

Species Distribution and Seasonality

Our results confirm the findings of early naturalists (Heller, 1909, 1910; Swarth, 1911; Grinnell, 1918; Miller and Allen, 1928) that *M. lucifugus*, *M. keenii*, *M. californicus*, and *M. volans* are regular members of the Southeast Alaska fauna. We confirm that *L. noctivagans* occurs regularly in Southeast Alaska (Barbour and Davis, 1969), but question whether this species occurs elsewhere in the state. We also question whether *E. fuscus* occurs regularly in Alaska because it is documented only by a single specimen far outside the known range of this species.

Species richness of bats is highest in Southeast Alaska, where they constitute 13% of the terrestrial mammal species. None of the species is abundant, however. *M. lucifugus* occurs throughout most of the forested regions of Alaska and has been captured in a wide variety of locations at least as far north as 65°N. *M. volans*, *M. californicus*, *M. keenii*, and *L. noctivagans* appear to reach their northern limits south of 59°N, in the temperate rainforests of Southeast Alaska, although *M. californicus* and *L. noctivagans* occur at more northerly locations in British Columbia.

According to Rapoport's rule (Rapoport, 1982; Stevens, 1989), there is a positive correlation between the highest latitude at which a species occurs and the latitudinal extent of its range. Wide temperature ranges and extreme cold at high latitudes favor species with wide climatic tolerance, allowing them to occupy larger geographical ranges. High-latitude species often are less restricted in the habitats they occupy (Stevens, 1989). *M. lucifugus* is such a species, occurring farther north than any other bat species in North America. The success of this species appears to result from a tolerance of a wide range of climatic conditions, a wide variety of prey species (Buchler, 1976; Anthony and Kunz, 1977; Whitaker and Lawhead, 1992; Parker, 1996), and a wide variety of roost types (Barclay and Cash, 1985; Nagorsen and Brigham, 1993; Kalcounis and Hecker, 1996; Vonhof and Barclay, 1996).

M. lucifugus occurs year-round in southern Alaska. We have found this species hibernating in caves in Southeast Alaska, and it has been collected on Kodiak Island in February (USNM). We do not know whether *M. lucifugus* migrates from the northern latitudes of central Alaska to hibernate in milder regions along the southern coast. Bats have been observed at Fairbanks as late as early October and as early as 7 May, just after river ice breakup (C.T. Seaton, pers. comm.

1994), suggesting that *M. lucifugus* may not travel far to hibernate. Alternatively, this species would have to migrate more than 400 km across the Alaska and Chugach mountain ranges to milder coastal regions. *M. lucifugus* in Ontario and the northeastern United States migrates up to 275 km to hibernate (Davis and Hitchcock, 1965; Fenton, 1970). In contrast, species of *Myotis* in the central and northern parts (north to 61°N) of the former Soviet Union hibernate in caves within their summer range (Strelkov, 1969), although seasonal migrations may occur between summer and winter portions of their annual range. *M. lucifugus* in Kentucky and Indiana appear to do both (Humphrey and Cope, 1976); thus it is possible that some *M. lucifugus* in central Alaska migrate long distances, whereas others hibernate within their summer range.

We suspect that *M. keenii*, *M. californicus*, and *M. volans* inhabit Southeast Alaska year-round, although it is difficult to confirm this with the small number of specimens collected. *M. californicus* and *M. volans* are nonmigratory elsewhere (Barbour and Davis, 1969). *M. keenii* inhabits coastal old-growth forests in Alaska, British Columbia, and Washington (van Zyll de Jong, 1985; van Zyll de Jong and Nagorsen, 1994; Parker and Cook, 1996). Because this rare species has not been documented outside the Pacific coast forest ecosystems, it is presumably nonmigratory as well.

Although *L. noctivagans* is difficult to capture, specimens indicate that females occupy Southeast Alaska in winter, possibly because of its mild, maritime climate. None of the echolocation calls we recorded in Southeast Alaska during the summer (Parker et al., 1996) were *L. noctivagans*. Whether females migrate to Southeast Alaska in winter, as specimen records suggest, or whether both sexes occur there throughout the year, as in southwestern British Columbia (Schowalter et al., 1978), is not known. We were not successful in substantiating reports that this species occurs in south-central Alaska (Manville and Young, 1965; cited in Hall, 1981).

We could not locate any specimens documenting *E. fuscus* in Southeast Alaska (Manville and Young, 1965). While *E. fuscus* is difficult to capture because it flies high, our analysis of echolocation calls in Southeast Alaska failed to identify a single *E. fuscus* call. We have no explanation for the lack of *E. fuscus* in Southeast Alaska; this species occurs at the same latitude and farther south along the coast in British Columbia (Nagorsen and Brigham, 1993; Wilkinson, 1995). The only specimen known from Alaska was most likely transported there by vehicle on the Alaska Highway (Reeder, 1965).

Environmental Factors

Availability of summer and winter roosts limits the distribution and abundance of bats in temperate climates (Humphrey, 1975; Kunz, 1982a). Natural roosts of *M. lucifugus*, *M. volans*, *M. californicus*, *M. keenii*, and *L. noctivagans* are located under loose bark or in snags and hollow trees (Kunz, 1982b; Barclay and Cash, 1985; Christy and West, 1993; Barclay and Brigham, 1996). The temperate rainforests of Southeast Alaska contain abundant live trees,

snags, and fallen logs in a variety of sizes (Alaback, 1991), which provide suitable hollows for cavity-roosting species. Although Alaska has a sparse human population, *M. lucifugus* commonly roosts in human-made structures during summer.

Extensive karst formations in Southeast Alaska (Buddington and Chapin, 1929; Baichtal, 1993) also provide numerous caves where hibernating bats have been observed and collected. Hot springs occur throughout this region (Waring, 1917; Motyka and Moorman, 1983), and bats roost at geothermally heated sites in Southeast Alaska, as well as in the Queen Charlotte Islands (Nagorsen and Brigham, 1993). Such roosts provide thermal advantages, and their importance as maternity roosts needs to be investigated. The abundance of different roost types suggests that hibernacula and summer roosts do not limit the distribution of bats in Southeast Alaska.

Lack of roosts probably limits bat distribution elsewhere in the state. To the north, forests are less dense and trees are smaller, limiting summer roosts. Bat distribution is likely constrained by the limit of the tree line, although a few records in southwestern Alaska (Iliamna Lake, Pedro Bay, Larsen Bay) indicate the occurrence of bats in habitats that lack large trees. Others also have found the occurrence of forests is correlated with the distribution of bats at northern latitudes (Ahlén, 1983; Ekman and de Jong, 1996), even when the bats inhabit buildings above the Arctic Circle (Rydell et al., 1994). This relationship appears to be important, and roost structure (Humphrey, 1975) and cover for predator avoidance (Rydell and Speakman, 1995) are likely contributing factors.

Because the temperature of deep caves tends to approximate the mean annual temperature at the surface (Tuttle and Stevenson, 1978), hibernation sites may be uncommon where the mean annual temperature is below 0°C. The availability of caves is limited in central Alaska, but limestone formations in interior Alaska (Blodgett and Gilbert, 1983; Gilbert et al., 1990) near the 0°C isotherm may contain caves suitable for hibernation. A *Myotis lucifugus* skeleton (UAM 30213) collected from a cave near the Chitistone River (between the Copper River and the U.S.-Canada border) suggests an attempt to hibernate where the mean annual temperature is below 0°C (Hartman and Johnson, 1984). In view of the ability of at least some *M. lucifugus* to tolerate temperatures as low as -4°C during hibernation (Webb et al., 1996), it is possible that the 0°C isotherm is too conservative a measure to apply in seeking hibernacula. Winter surveys of caves and buildings are needed to delineate the northern extent of hibernation by *M. lucifugus* in central, southwestern, and south-central Alaska. In this regard, it is relevant that *M. lucifugus* is not known to hibernate in buildings in other parts of its range (Nagorsen and Brigham, 1993).

In addition to temperature, precipitation may affect the distribution of bats in Southeast Alaska, where the average amount ranges from 1000 to 8100 mm annually (Hartman and Johnson, 1984). In similar temperate rainforests on the western slopes of the Cascade Mountains of Oregon, Thomas (1988) found that the sex ratio of *M. lucifugus* was skewed

toward male bats, and females were nonreproductive. He concluded that this difference was due to extended periods of rain, which limited foraging opportunities and forced bats into torpor. Pregnant and lactating females cannot fully use the energy savings of torpor (Kurta, 1990). However, the equal sex ratio of *M. lucifugus* in Southeast Alaska demonstrates that females tolerate the wet climate. Precipitation also decreased reproductive success of this species during rainy years in more arid regions of British Columbia (Grindal et al., 1992). Although the ratio of reproductive to nonreproductive females in Southeast Alaska is not known, the occurrence of maternity colonies demonstrates that *M. lucifugus* females are able to raise young in this cool, rainy climate.

Geographic barriers bordering Southeast Alaska possibly limit bat distribution. This region is isolated from south-central Alaska and British Columbia by the extensive ice fields of the St. Elias and Coast mountains. These mountains are a barrier for other mammals (Klein, 1965; MacDonald and Cook, 1996), although major river valleys may provide corridors for dispersal for some species (Klein, 1965). In addition, the effect of the highly fragmented Alexander Archipelago on bat occurrence and movement in Southeast Alaska is unknown. Island isolation is known to influence distribution of bat species in Scandinavia (Ahlén, 1983; Johansson and de Jong, 1996). Further documentation of bat distribution in the Alexander Archipelago is necessary to elucidate latitudinal and island biogeographical gradients in species richness in Southeast Alaska.

Because bats are nocturnal, the decreased length of summer nights at high latitudes may limit their northern distribution. Bats minimize the risk of diurnal avian predators by foraging during the darkest hours (Baker, 1962; Byre, 1990; Rydell and Speakman, 1995). At 65°N in central Alaska, the sun is below the horizon less than 2.2 h each night during late June, and full darkness does not occur until August. At this latitude, we have observed *M. lucifugus* in June foraging just above 3–5 m tall willows (*Salix* spp.) along calm water in the late evening and early morning (2330–0230 local time). Farther north, short nights could prevent bats from acquiring enough energy (Anthony and Kunz, 1977) or calcium (Barclay, 1994) to meet the needs of pregnancy and lactation. At 55°N in Southeast Alaska, bats do not forage until after sunset and complete most flight activity 3 h before sunrise (Parker et al., 1996). Night length (6.5 h from sunset to sunrise on 21 June) apparently does not limit foraging time in Southeast Alaska. Rydell (1989) has documented bats at high latitudes beginning and ending their foraging flights in daylight, suggesting that bats can compensate to some extent for limited darkness. The effect of night length on the latitudinal gradient of bats in Alaska needs to be further evaluated.

Bats are affected by prey availability, and insect abundance tends to decrease in cool or rainy weather (Johnson, 1969). Spiders composed 15% of the estimated diet volume of *M. lucifugus* in Southeast Alaska (Parker, 1996) and 16% in central Alaska (Whitaker and Lawhead, 1992). Although *M. lucifugus* feeds on a variety of prey, it does not normally eat spiders in the more southerly parts of its range (Whitaker,

1972; Buchler, 1976; Fenton and Morris, 1976; Whitaker et al., 1977; Whitaker et al., 1981) and does not glean prey from foliage (Barclay, 1991). Exploitation of prey not consumed elsewhere may enable *M. lucifugus* to reproduce in Southeast Alaska and extend its range north to central Alaska. Further investigation of the diet of *M. lucifugus* and other bats in Alaska, including the availability of prey items, is needed to evaluate this possibility.

CONCLUSION

Our study refines the range and distribution limits of the six bat species in Alaska. *M. lucifugus* is the widest ranging species; it inhabits a broad range of environments, from wet temperate forests in Southeast Alaska to boreal forest with short summer nights in central Alaska. *E. fuscus* does not appear to occur regularly in Alaska. *M. keenii*, *M. californicus*, *M. volans*, and *L. noctivagans* are regular members of the Southeast Alaska fauna (south of 59°N). All five bat species in Southeast Alaska probably inhabit the region year-round, with the possible exception of *L. noctivagans*. Because of the milder winters in this coastal region, *L. noctivagans* may migrate from interior British Columbia to Southeast Alaska in winter. We remain uncertain whether *M. lucifugus* in central Alaska migrates to hibernate in milder southern regions or hibernates within its summer range.

Bat diversity in Alaska declines sharply at about 59°N. Factors that may influence bat distribution in Alaska include geography, night length, precipitation, and prey abundance. We think the factors having the greatest influence are temperature, the availability of summer and winter roosts, and the extent of forested habitat. These factors all need to be investigated further to evaluate their relative influences on the latitudinal gradient of bats at the northern limits of their ranges. Current research is now focusing on these factors, particularly the influence of forest parameters on bat distribution.

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APPENDIX. LIST OF MUSEUM SPECIMENS
AND LOCALITY

Specimens were provided by the following museums: Alaska Department of Fish and Game Collection, Anchorage, Alaska (ADMC); American Museum of Natural History (AMNH); Carnegie Museum of Natural History (CM); Field Museum of Natural History (FMNH); Los Angeles County Museum (LACM); Museum of Comparative Zoology, Harvard University (MCZ); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Royal Ontario Museum (ROM); University of Alaska Museum (UAM); University of Illinois Museum of Natural History (UIMNH); University of Kansas Museum of Natural History (KU); University of Michigan Museum of Zoology (UMDZ); U.S. National Museum of Natural History (USNM).

***Myotis lucifugus* (Le Conte, 1831)**

Central Alaska (20 specimens). Minto L., 65°00'N 148°30'W (4 UAM); Smallwood Cr., 64°55'N 147°15'W (1 UAM); 18 mi. Old Nenana Hwy., 64°51'N 148°15'W (1 UAM); College, 64°50'N 147°50'W (2 UAM, 1 UMDZ); Fairbanks, 64°50'N 147°30'W (1 UAM); North Pole, 64°45'N 147°21'W (4 UAM); 5 mi. S of North Pole, 64°N 147°W (1 UAM); Harding L., 64°45'N 146°50'W (2 MVZ); Bonanza Cr. Experimental Forest, 64°42'N 148°16'W (1 UAM); Sleetmute, 61°42'N 157°10'W (1 CM); Birch L., 64°20'N 146°20'W (1 UAM).

Southwestern Alaska (51 specimens). Mainland: Pedro Bay, 59°42'N 154°13'W (1 CM); Iliamna Lake, 59°30'N 154°4'W (1 USNM); King Salmon, 58°41'N 156°39'W (1 UAM). Afognak I.: Kitoi Bay, 58°11'N 152°21'W (1 CM). Kodiak I.: 57°20'N 153°22'W (9 USNM, 1 MCZ); Chiniak, 57°37'N 152°10'W (18 UAM); Uyak Bay at Larsen Bay, 57°32'N 153°58'W (5 FMNH, 14 KU).

South-central Alaska (23 specimens). Palmer, 61°36'N 149°6'W (2 CM); Chitistone R., 61°26'N 142°31'W (1 UAM); Anchorage, 61°13'N 149°53'W (1 USNM, 1 FMNH, 1 UIMNH); Peters Cr., 61°24'N 149°26'W (1 KU); Port Nellie Juan, 60°33'N 148°9'W (1 MVZ); Hope, 60°55'N 149°38'W (2 CM); Cordova, 60°30'N 145°25'W (10 UAM); 6 mi. S of Wasilla, 61°N 149°W (3 UIMNH).

Southeast Alaska (185 specimens). Mainland: Bartlett Cove, 58°27'N 135°53'W (10 UAM); Situk R., 59°26'N 139°33'W (2 ROM); Juneau near Salmon Cr., 58°37'N 134°27'W (1 UAM); Andrew Cr., N of Mt. Rynda, 56°40'N 132°13'W (5 UAM); Bailey Bay Hot Spr., 55°58'N 131°37'W (1 UAM); Marten Arm of Boca de Quadra Fjord, 55°10'N 130°31'W (3 MVZ); Salmon R. at Fish Cr., 55°58'N 130°2'W (5 UAM); Hyder, 55°55'N 130°1'W (40 UAM); Mouth of Chickamin R., 55°49'N 130°54'W (3 UAM); Hugh Smith L., 55°6'N 130°40'W (3 UAM). Chichagof I.: Hoonah, 58°06'N 135°26'W (20 UAM); White Sulphur Spr., 57°6'N 134°20'W (4 UAM); Kadashan R., 57°42'N 135°13'W (1 UAM). Admiralty I.: Windfall Harbor 57°50'N 134°18'W (4 UAM); Mole Harbor, 57°40'N 134°3'W (1 MVZ). Baranof I.: Sitka, 57°3'N 135°20'W (6 USNM, 1 MCZ, 2 CM); Red Bluff Bay, 56°50'N 134°42'W (8 MVZ, 2 KU). Mitkof I.: Petersburg Reservoir, 56°55'N 133°47'W (1 UAM); Petersburg, 56°48'N 132°58'W (6 UAM). Wrangell I.: Fool's Inlet Rd., 56°17'N 132°5'W (1 UAM). Prince of Wales I.: Red Cr., 56°15'N 133°20'W (3 UAM); northern Prince

of Wales Island caves, 56°13'N 133°W (9 UAM); Turn Cr., 56°10'N 133°18'W (1 UAM); 108 Cr., 56°8'N 133°8'W (5 UAM); Polk Inlet, 55°20'N 132°30'W (3 UAM); Dog Salmon Cr., 55°19'N 132°28'W (2 UAM); Nichols L., 54°45'N 132°11'W (1 UAM). Revillagigedo I.: Portage Cove, 55°46'N 131°2'W (14 MVZ); Loring, 55°36'N 131°39'W (4 UAM, 4 USNM); Ward L., 55°24'N 131°42'W (3 UAM); Ketchikan, 55°20'N 131°38'W (3 USNM); Herring Bay, 55°20'N 131°31'W (1 UAM). Grant I.: 55°33'N 131°43'W (1 LACM). Dall I.: Essowah L., 54°47'N 132°52'W (1 UAM).

***Myotis volans* (H. Allen, 1866)**

Southeast Alaska (5 specimens). Admiralty I.: Mole Harbor, 57°40'N 134°3'W (1 MVZ). Wrangell I.: Mt. Dewey trail head, 56°28'N 132°23'W (2 UAM, 1 ADMC). Prince of Wales I.: Polk Inlet, 55°20'N 132°30'W (1 UAM).

***Myotis keenii* (Merriam, 1895)**

Southeast Alaska (3 specimens). Chichagof I.: Hoonah, 58°6'N 135°26'W (1 UAM). Wrangell I.: Wrangell, 56°28'N 132°22'W (1 USNM). Prince of Wales I.: Turn Cr., 56°10'N 133°18'W (1 UAM).

***Myotis californicus* (Audubon and Bachman, 1842)**

Southeast Alaska (5 specimens). Prince of Wales I.: El Capitan Cave, 56°10'N 133°19'W (3 UAM). Long I.: Howkan, 54°52'N 132°48'W (2 MVZ).

***Lasionycteris noctivagans* (Le Conte, 1831)**

Southeast Alaska (4 specimens). Mainland: Taku River, Canyon I., 58°43'N 133°40'W (1 AMNH). Wrangell I.: 15 km S of Wrangell, 56°22'N 132°22'W (1 UAM). Mitkof I.: Petersburg, 56°45'N 132°56'W (1 UAM). Revillagigedo I.: 4 mi. N Tongass Hwy., Ketchikan, 55°20'N 131°38'W (1 UAM).

***Eptesicus fuscus* (Palisot de Beauvois, 1796)**

Central Alaska (1 specimen). Shaw Creek, 64°16'N 146°6'W (1 UMDZ).

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