Journal of Mammalogy, 84(2) 579–593, 2003

SEASONAL DISTRIBUTION OF MIGRATORY TREE BATS (*LASIURUS* AND *LASIONYCTERIS*) IN NORTH AMERICA

PAUL M. CRYAN*

United States Geological Survey, Arid Lands Field Station, Fort Collins Science Center, Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA

Despite evidence of migration in North American tree bats (genera *Lasiurus* and *Lasionycteris*), details regarding seasonal movements in these widely distributed species are few. This study attempted to clarify patterns of seasonal distribution by mapping museum occurrence records by month. Monthly changes in the distribution of records indicate seasonal movements of tree bats. Northward migration during spring by *Lasiurus cinereus* appears to stem from wintering grounds in California and Mexico. During summer, male *L. cinereus* is mainly distributed in western North America, whereas females dominate samples from eastern regions. *Lasiurus borealis* winters in southeastern areas and expands its range into more northern regions during warmer months. Seasonal dispersal of *Lasiurus blossevillii* from California is apparently limited, and it is unclear if this group mixes with others to the south and east. *Lasionycteris noctivagans* also shows movement at the continental scale, although movements may differ between western and eastern groups. Museum records provide little evidence of major movement by any species between North and South America. Despite inherent biases, museum records are a viable means of investigating bat migration.

Key words: Chiroptera, *Lasionycteris noctivagans*, *Lasiurus blossevillii*, *Lasiurus borealis*, *Lasiurus cinereus*, migration, occurrence records, seasonal distribution

Bats are among the few terrestrial small mammals capable of escaping seasonally harsh conditions by moving rapidly over long distances (>100 km) to more favorable areas. Despite this potential to occupy different regions over the course of a year, our understanding of seasonal distribution and movement in many species of bats is incomplete. Range maps of mammal distributions typically depict areas in which a species is known to occur and usually include records gathered throughout the year. Such maps do not account for seasonal variation in distribution, which can be problematic for bats (Hoffmeister 1970). Further compounding the problem of seasonal variation in range, male and female bats often differ in distribution at both local (Cryan et al. 2000) and larger scales (Findley and Jones 1964). Differences in distribution between sexes are often noted, typically as skewed sex ratios in local studies, but rarely mapped or quantified across the entire range of a species. A necessary step toward understanding the ecology or conservation status of bats is developing a thorough understanding of their seasonal movement patterns and how these movements differ between the sexes. Clarification of seasonal distributions may be particularly important for bats that are widely distributed, show skewed sex ratios at local scales, or make long-distance movements between seasons.

Several species of the genera *Lasiurus* and *Lasionycteris*, commonly referred to as tree bats for their propensity to roost in the foliage or trunks of trees (Griffin 1970), are

* *Correspondent: paul_cryan@usgs.gov*

presumed to be highly migratory (Barbour and Davis 1969). These species are hoary bats (*Lasiurus cinereus*), western and eastern red bats (*Lasiurus blossevillii* and *Lasiurus borealis*, respectively—see Baker et al. 1988; Morales and Bickham 1995), and silver-haired bats (*Lasionycteris noctivagans*). Circumstantial evidence of migration in tree bats began accumulating over 150 years ago (Howell 1908; Jones 1884; Linsley 1842; Mearns 1898; Merriam 1887; Miller 1897; Rhodes 1903).

Evidence of migration in *L. cinereus* typically involves its appearance on remote islands and distant locations. These occurrences include scattered records from Bermuda (Jones 1884; Van Gelder and Wingate 1961), Newfoundland (Maunder 1988), the Northwest Territories, Canada (Hitchcock 1943), Iceland (Hayman 1959), and the Orkney Islands off the coast of Scotland (Hill and Yalden 1990). In addition to these records of apparently wayward migrants, other evidence of migration includes diurnal flocks (Hall 1946; Howell 1908), collisions with buildings (Saunders 1930; Timm 1989), and the regular appearance of hoary bats on the Farallon Islands (Tenaza 1966; P. Pyle, pers. comm.), which are approximately 32 km off the coast of California. The majority of these encounters occur during autumn. Although reports of apparently migratory *L. borealis* are known from spring, most encounters also occur in autumn. Examples of encounters with *L. borealis* that were apparently migrating include diurnal flocks (Mearns 1898), seasonal peaks in local abundance (Barclay 1984), bats landing on ships at sea (Carter 1950; Mackiewicz and Backus 1956; Norton 1930; Peterson 1970; Thomas 1921), collisions with buildings (Crawford and Baker 1981; Saunders 1930; Terres 1956; Timm 1989), and occasional appearances on Bermuda (Jones 1884; Van Gelder and Wingate 1961). Observations of migration in *L. blossevillii* are few, but evidence indicates that seasonal movements may occur in California (Constantine 1959; Grinnell 1918) and that *L. blossevillii* moves south out of New Mexico during winter (Findley et al. 1975). Evidence of migration in *L. noctivagans* includes records of bats landing on ships at sea (Mackiewicz and Backus 1956; Thomas 1921), seasonal peaks in local abundance (Barclay et al. 1988; Bogan and Cryan 2000), collisions with buildings (Saunders 1930), and their occasional appearance on Bermuda (Van Gelder and Wingate 1961).

Despite such evidence of migration in tree bats, few studies have detailed their seasonal movements in North America. Much of what we know about movement in tree bats comes from observations of different researchers working in relatively limited areas and during different seasons. Notwithstanding the scope of these individual observations, when compiled, they can reveal general trends in seasonal distribution. The most comprehensive study to date on movement in tree bats used museum records to map the seasonal distribution of hoary bats at the continental scale (Findley and Jones 1964). This method proved successful in uncovering previously undocumented patterns of distribution and potential movement of *L. cinereus*, but there have been few subsequent efforts of its kind. In hopes of expanding on the work of Findley and Jones (1964) and clarifying the seasonal distributions of other species, I used a similar method and mapped the monthly distribution of museum occurrence records of *L. borealis*, *L. blossevillii*, *L. cinereus*, and *L. noctivagans* in North America.

Materials and Methods

I requested data pertaining to species, sex, age, reproductive status, capture date, and capture locality from specimens of *L. noctivagans* and *Lasiurus* species housed in mammal collections throughout the Americas. Specimen records were incorporated into a computer database. Geographic coordinates were assigned to each record based on place names that were recorded as the collection locality; latitude and longitude coordinates were assigned to each record using the United States Geological Sur-

vey's Geographic Names Information Server (GNIS at Internet site http://geonames.usgs.gov/index.html) for localities in the United States, the Geographical Names Board of Canada's name server (http://geonames.nrcan.gc.ca) for sites in Canada, and the United States National Imagery and Mapping Agency's GEOnet Names Server (http://164.214.2.59/gns/html/index.html) for all other countries. Records were categorized by species and mapped for both male and female bats using a geographic information system (GIS—ARC/INFO 8.1, ArcView 8.1, Environmental Systems Research Institute, Redlands, California). Records with no specific locality information were mapped in the center of the state or county from which they came. Records for which there were no associated date or sex, data were not mapped. All maps are presented in Lambert-azimuthal projection (center latitude 45°, center longitude −110°). There is a broad area of potential sympatry between *L. borealis* and *L. blossevillii* in western Texas, New Mexico, and Mexico (Genoways and Baker 1988; Ramírez-Pulido and Castro-Campillo 1994; Valdez et al. 1999). Because I have not examined specimens from areas of potential sympatry, identifications from these regions should be treated cautiously. Only data from sources associated with museum voucher specimens were included in this analysis. Multiple individuals were collected from many of the localities shown in Figs. 1–3. Therefore, areas of relatively high record density for each month and sex were computed and mapped using the density analysis function of ArcView Spatial Analyst software (Environmental Systems Research Institute). Areas of relatively high density were delineated by taking the range of available density values for each month and sex, classifying that range of values into 4 equal-interval categories, and then plotting the extent of the highest-value category. These density areas are relative to the number of records available for a given sex each month and are not comparable among months or between sexes. Because the focus of this article is movement of tree bats in North America, Nearctic seasons are implied: spring (March–May); summer (June–August); autumn (September–November); winter (December–February).

Results and Discussion

Data were acquired from 127 mammal collections (Appendix I) throughout North and South America. Records for which there were adequate locality and sex data (Figs. 1–3) are as follows: *L. cinereus* (n = 3,217); *L. blossevillii* (n = 935); *L. borealis* (n = 4,778); *L. noctivagans* (n = 1,627). Although museum records offer a convenient and previously underused means of mapping the seasonal distributions of bats, interpretation of these data should be treated cautiously. Museum records indicate presence only; absence of records from an area does not necessarily mean that bats do not occur there. Biases associated with variable collection techniques (e.g., shooting or hand capture versus netting) and variation in seasonal activity levels of both bats and biologists must also be considered. For example, many of these bats are likely capable of torpor or hibernation (Genoud 1993; Kunz 1982), and some of the northward progression of records during spring may simply indicate previously dormant individuals becoming active with the northward progression of warm temperatures (Baker 1978). Other potential biases to these data likely include underrepresentation of records from seasons during which biologists are not conducting fieldwork or lack of records from areas where specimen collection is not commonly practiced. In addition, the age and reproductive condition of bats may also affect likelihood of encounter (e.g., pregnant females and juveniles may be more likely to be captured). Despite these inherent biases of museum records, other trends in the data, such as the summer disappearance of records from wintering areas or disappearance of only 1 sex from an area, probably indicate actual movement patterns. Regardless of potential biases, museum records are abundant, verifiable, and relatively traceable since the advent of GIS technology. Consolidation and analysis of such data present a coarse yet underused means of studying bat distribution.

Lasiurus cinereus.—Hoary bats range throughout the Americas from northern Canada south to Argentina and Chile (Hall

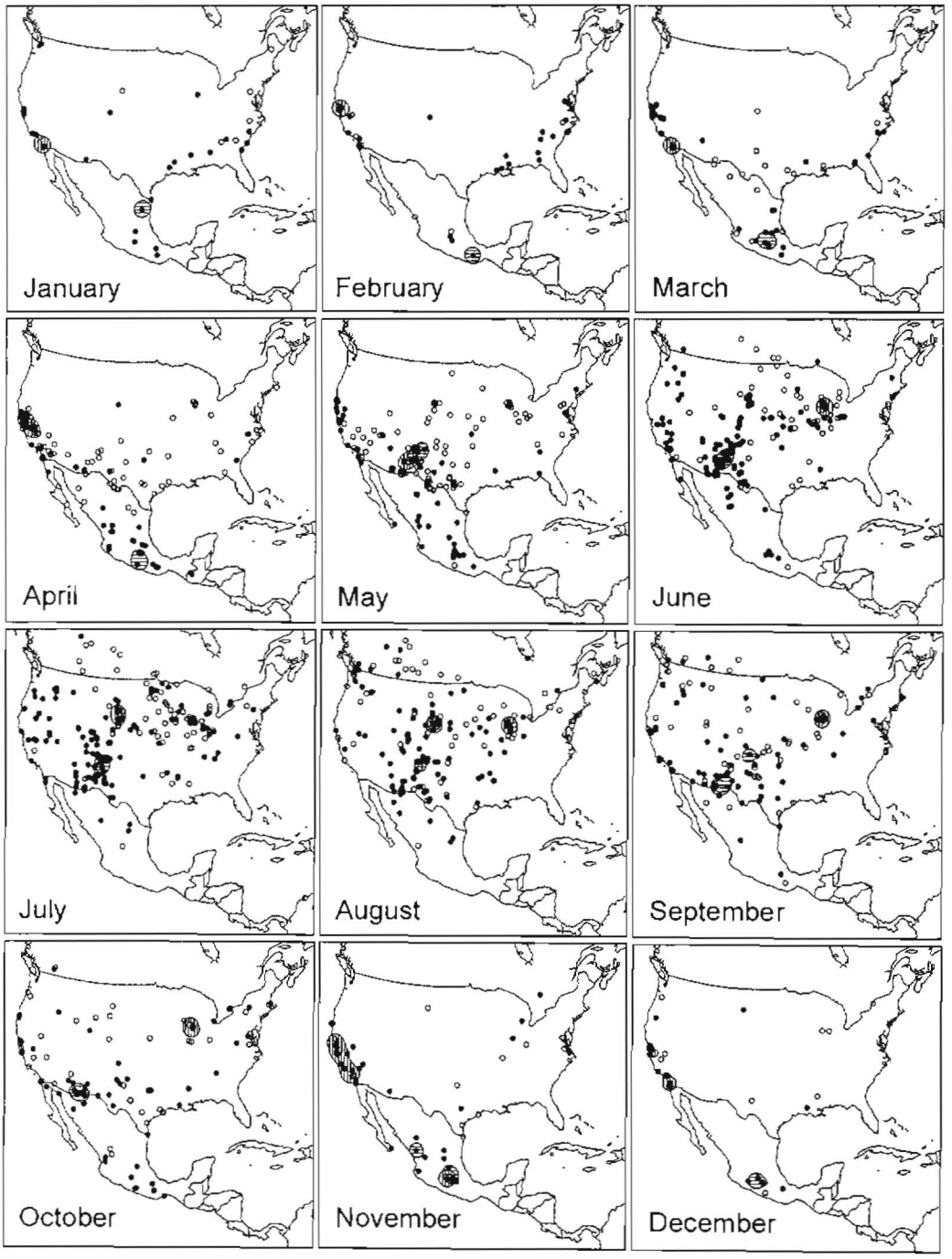

FIG. 1.—Monthly distribution of hoary bats (*Lasiurus cinereus*) in North America, occurrences based on museum records; closed circles = males, open circles = females. Hatched areas represent regions with the highest number of occurrences per unit area; horizontal hatching = areas of high male density, vertical hatching = areas of high female density. See "Materials and Methods" section for description of density calculation.

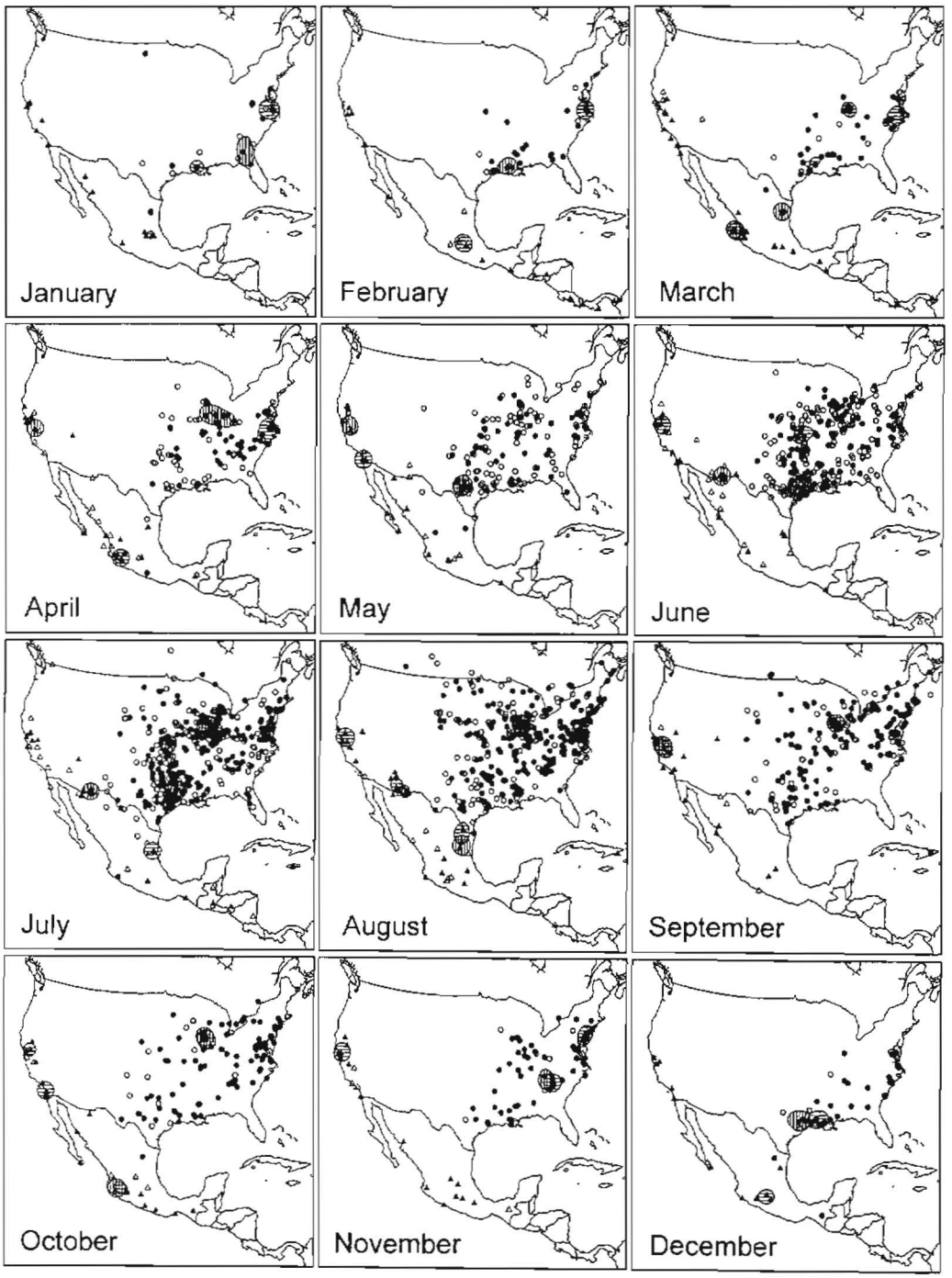

FIG. 2.—Monthly distribution of red bats (*Lasiurus borealis* and *Lasiurus blossevillii*) in North America. occurrences based on museum records; closed circles = male *L. borealis*, open circles = female *L. borealis*, closed triangles = male *L. blossevillii*, open triangles = female *L. blossevillii*. Hatching as in Fig. 1. See text for description of density calculation.

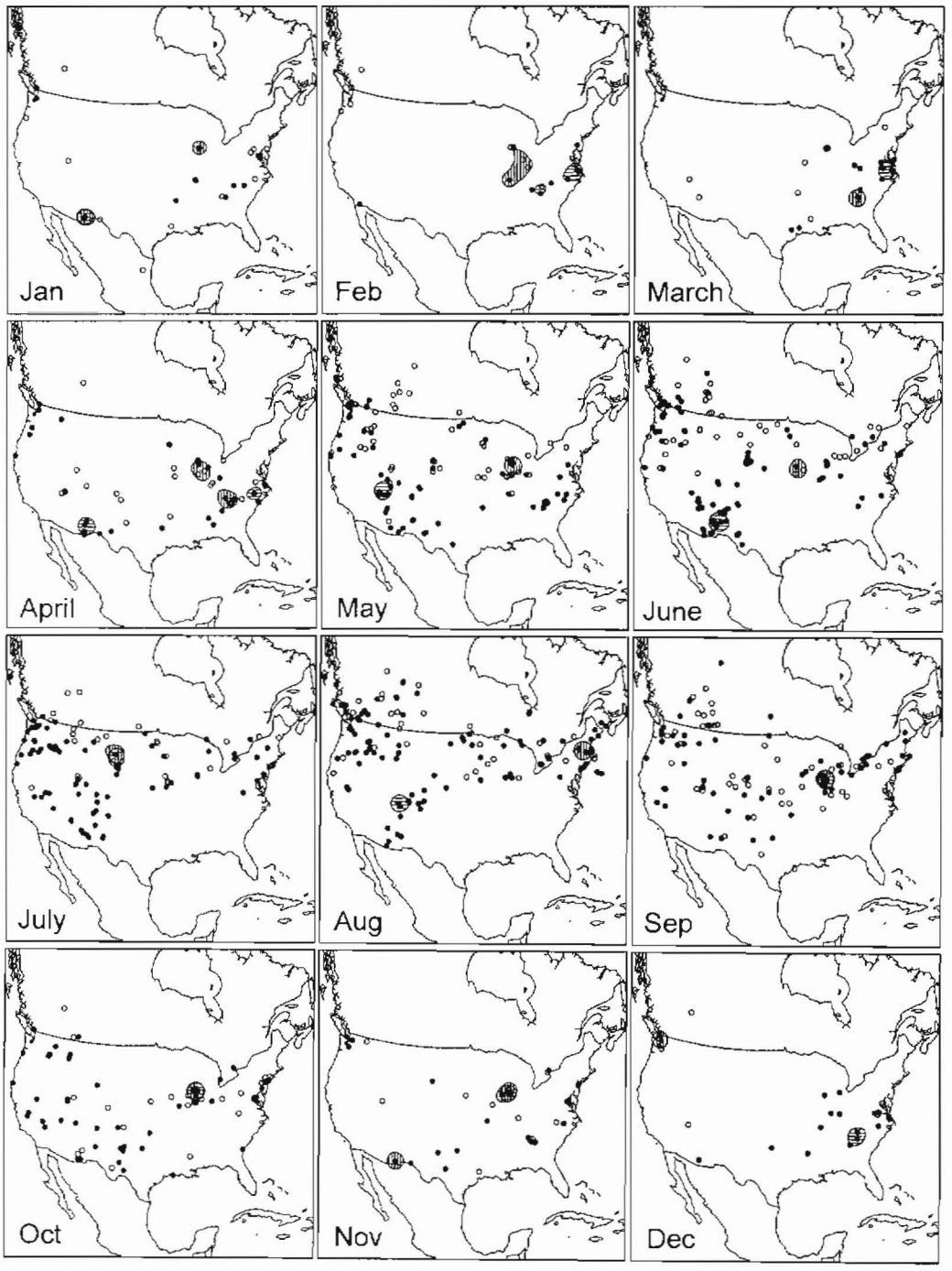

FIG. 3.—Monthly distribution of silver-haired bats (*Lasionycteris noctivagans*) in North America, occurrences based on museum records. Symbols and hatching as in Fig. 1. See text for description of density calculation.

1981; Shump and Shump 1982b). During winter, they are found at scattered localities throughout North America, including eastern regions of the United States, California (Findley and Jones 1964), and Mexico (Polaco et al. 1992; Watkins et al. 1972). Records from winter in the eastern half of the continent (n = 48) are widely dispersed, whereas records during this season from California (n = 71) and Mexico (n = 47; Fig. 1) are more concentrated. Before confirmation that *L. cinereus* occurred in Mexico during winter, Findley and Jones (1964:470) suspected that "an extensive undetected wintering population of hoary bats exists south of the United States." However, the importance of Mexico and points farther south as wintering areas for *L. cinereus* remains undetermined. Although records show that overwintering occurs in Mexico, available evidence does not indicate that both sexes frequent Mexico during winter. Records of male *L. cinereus* during winter (n = 43) outnumber those of females (n = 4) in Mexico, whereas sex ratios in California during winter are more even (n = 38 males, 33 females). California was also the only state in the United States from which there were more than 3 records of both male and female *L. cinereus* during winter.

During spring, *L. cinereus* has been captured in concentrated groups (>20 per night) in southern California (Vaughan 1953), Arizona (Mumford 1963), and New Mexico (Findley and Jones 1964), suggesting migratory movements through these areas. Although such concentrations may represent migratory "waves" moving toward their summer quarters, the origins of these migrants are unclear. A paucity of records of females from Mexico during winter and spring does not support the contention that all these spring migrants are coming from Mexico. It seems more likely that some *L. cinereus*, particularly females, observed in southwestern United States during spring are migrants moving east from wintering grounds in California. Given available data, this is the most parsimonious explanation for the lack of records of females from Pacific coastal regions during spring and summer (Dalquest 1943). Whereas records show that male *L. cinereus* disperses north from California during spring, there are no records of females from regions north of California between March and July. Furthermore, there are fewer records of females from California in summer (n = 7) than during any other season. This apparent lack of female *L. cinereus* in California and the Pacific Northwest during summer remains a mystery. Although males apparently move to higher elevations during summer (Dalquest 1943; Vaughan and Krutzsch 1954), there is little evidence that females give birth and raise young in California (E. D. Pierson, pers. comm.).

In summer, *L. cinereus* is found in many parts of the United States and in the southern half of Canada, although it is relatively uncommon during this time east of the Mississippi River and south of the Ohio River (Findley and Jones 1964; Zinn and Baker 1979; Fig. 1). Reasons for this lack of records from the southeastern United States from the months of June through September remain unclear. Distribution of the sexes during summer is relatively segregated; males occur primarily in mountainous regions of western North America, whereas females occupy more eastern areas (Findley and Jones 1964; Fig. 1). However, adults of both sexes occur during summer in the Black Hills and surrounding areas of the Great Plains (Bogan and Cryan 2000; Czaplewski et al. 1979; Jones et al. 1973; Sparks and Choate 2000; Turner 1974). Parturition in *L. cinereus* generally ranges from mid May to early July (Shump and Shump 1982b), and scattered records of males in more eastern areas during summer may represent young-of-year (Findley and Jones 1964). However, presence of adult males in eastern parts of the range during summer is likely.

Distribution of records indicates coastward movement during late summer, although movement toward the Pacific Coast

is more pronounced than movement toward the Atlantic Coast. Records of females along the northern Pacific Coast during August suggest their arrival from points east and north. Both sexes of *L. cinereus* occur on the Farallon Islands off the coast of California during autumn (Tenaza 1966), and copulatory activity has been observed there (P. Pyle, pers. comm.). It remains to be determined where female *L. cinereus* migrating down the Pacific Coast in autumn spend spring and summer. Given the potential for the Rocky Mountains to serve as a barrier to dispersal, some female *L. cinereus* may return to California by circumnavigating the Rocky Mountains to the north. Such a migration pattern would help to explain the lack of distinct autumn migratory waves in areas of southwestern United States that experience spring migrants in larger numbers (Findley and Jones 1964).

The museum records do not point to major movement by *L. cinereus* between North and South America. Lack of records from Central America, despite the relatively frequent detection of *L. blossevillii* in the region (Fig. 2), does not support the idea that migrants move through that area. Furthermore, there is little compelling evidence that migratory groups move into and out of the southeastern United States from the Caribbean. Although evidence exists of migratory movement through Florida during spring, records are limited and few females were involved (Zinn and Baker 1979). The level of genetic divergence (3.5%) found between *L. c. cinereus* from North America and *L. c. villosissimus* from South America (Morales and Bickham 1995) suggests limited exchange between continents and warrants further research concerning the specific status of these groups (Bradley and Baker 2001).

Lasiurus borealis.—Eastern red bats occur throughout much of eastern North America, generally east of the Continental Divide from southern Canada south to northeastern Mexico (Baker et al. 1988; Hall 1981; Ramírez-Pulido and Castro-Campillo 1994). During winter, *L. borealis* occurs throughout the southeastern United States and northeastern Mexico, but concentrations are highest in coastal Atlantic and Gulf of Mexico regions (Fig. 2). As pointed out by previous authors (Davis and Lidicker 1956; LaVal and LaVal 1979; Padgett and Rose 1991), males tend to be more common in northern areas during winter, whereas concentrations of females generally occur in more southern areas (Fig. 2).

During spring and summer, the range of *L. borealis* expands into the Great Lakes and the Great Plains regions (Baker 1978; Whitaker and Hamilton 1998), followed by further expansion to the north and west during summer (Fig. 2). Unlike *L. cinereus*, there are no clear differences in the distribution of male and female *L. borealis* at the continental scale during spring and summer. Skewed sex ratios observed in local studies during the warmer months (Czaplewski et al. 1979; Ford et al. 2002; Jones et al. 1967; Kunz 1971) probably are the result of differential distribution at smaller scales.

After apparent expansion onto the northern Great Plains by some *L. borealis* during August, movements during autumn are oriented toward the east and south (Fig. 2). Relatively high densities of *L. borealis* after June along the Atlantic Coast, north of New York City, may indicate shoreline migration during autumn. The high proportion of male records during late autumn in northern regions previously occupied by both sexes again suggests that some males may not migrate as far south as females during autumn. Although *L. borealis* disperses as far west as the Great Plains, the majority of records occur within more mesic (>90 cm of rain per year—Baldwin 1968) eastern areas. Arid regions of the western United States may limit dispersal of *L. borealis* from the east and possibly serve as a reproductive barrier between eastern and western species of red bats.

Lasiurus blossevillii.—Western red bats regularly occur in California, Arizona, New

Mexico, and throughout western and central Mexico to South America (Baker et al. 1988; Hall 1981; Ramírez-Pulido and Castro-Campillo 1994). Much of our understanding of *L. blossevillii* comes from studies in California, where it apparently resides year-round (Constantine 1959). Both sexes are together at lower elevations in California during winter (Grinnell 1918; Orr 1950) but segregate during spring and summer; females remain in lowland areas, whereas males apparently move to higher elevations (Grinnell 1918; Shump and Shump 1982a). *L. blossevillii* also winters in central Mexico (Fig. 2), but the lack of records from areas between California and Mexico makes it difficult to determine whether these wintering groups represent a continuous winter range or disjunct populations.

Female *L. blossevillii* gives birth and raises young in California and parts of southwestern New Mexico (Constantine 1959; Findley et al. 1975). Accumulation of records in southeastern Arizona and southwestern New Mexico during spring indicates movement into the region from elsewhere, most likely southern areas (Fig. 2). It appears as though Californian populations do not disperse out of the state during the year, and they may be resident there year-round, as suggested by Constantine (1959). Given the distribution of available records during summer, it is difficult to determine whether Californian breeding populations are continuous with populations to the south and east.

Morales and Bickham (1995) recommended that populations of *L. blossevillii* in North and Central America should be assigned to the subspecies *L. b. frantzii*. Based on this assignment, it would be expected that interchange occurs between California and other areas of southwestern United States and west-central Mexico. However, analysis by Morales and Bickham (1995) did not include specimens from California or anywhere else in the United States, and given the apparently limited movement of populations out of California, judgment concerning subspecific status of bats in California should be reserved until further study. Unlike any other species of *Lasiurus* studied, there are numerous (n = 39) records of *L. blossevillii* from countries in Central America. Although the close proximity of *L. b. frantzii* to South America makes movement onto that continent from the north seem likely, genetic studies provide evidence to the contrary. A relatively high level of genetic divergence (5.4%) between *L. b. frantzii* from North and Central America and *L. b. blossevillii* from South America provides evidence that these may be separate species (Bradley and Baker 2001; Morales and Bickham 1995). Additional genetic comparisons among populations of *L. blossevillii* throughout its range, including California, may help clarify migratory movements by establishing levels of genetic exchange between populations.

Lasionycteris noctivagans.—Silver-haired bats range from southeastern Alaska and much of Canada south to central California, northern Mexico, and east through Georgia (Hall 1981; Yates et al. 1976). *L. noctivagans* winters in the Pacific Northwest, in scattered areas of the southwestern United States, and at middle latitudes of the eastern United States, approximately south of Michigan and east of the Mississippi River (Izor 1979; Nagorsen et al. 1993; Szewczak et al. 1998; Tyler and Payne 1982; Fig. 3). There are occasional reports of *L. noctivagans* hibernating in caves, mines, and trees (Beer 1956; Cowan 1933; Gosling 1977; Nagorsen et al. 1993). Appearance of both sexes in southwestern United States in early spring indicates either arousal of previously dormant bats that winter in these regions or arrival of bats from other wintering grounds. However, captures from southern New Mexico reveal that both sexes are resident in that area during winter (W. Gannon, pers. comm.). With the progression of spring, it appears that populations of *L. noctivagans* from eastern parts of the range disperse east and north from wintering areas, whereas movement in

western parts of the range is northward. Records generally support earlier observations that, at least in eastern populations, males stay behind on some parts of the wintering range as females move north from southern wintering grounds (Whitaker and Hamilton 1998). As with *L. cinereus*, there are strikingly few records of *L. noctivagans* from the southeastern United States during spring and summer. Females begin moving south into areas occupied by males during late summer and early autumn, when the distributions of the sexes tend to overlap. As autumn progresses, the ranges of both sexes generally shift south. Appearance of records along northern parts of the Atlantic Coast during autumn shows that some *L. noctivagans* may migrate along coastlines.

One region consistently noted for relatively even sex ratios of *L. noctivagans* year-round is British Columbia, suggesting that migration does not occur in that area (Cowan 1933; Nagorsen et al. 1993; Schowalter et al. 1978). Given the distribution of records of *L. noctivagans* (Fig. 3), the possibility exists that populations of *L. noctivagans* in the Pacific Northwest and along the Pacific Coast are somewhat isolated from populations in more eastern regions. Circumstantial evidence in support of limited interchange between western and eastern populations includes disjunct distributions of bedbug species (*Cimex*—Kunz 1982; Usinger 1966) and the presence of an endemic flea (*Eptescopsylla vancouverensis*) on *L. noctivagans* in British Columbia (Jackson 1961). Further research into the relationships between western and eastern groups of *L. noctivagans* may facilitate interpretation of seasonal movements.

Overview.—Both *L. noctivagans* and *L. cinereus* exhibited differing distributions of the sexes on a continental scale during summer, but distributions of male and female *L. blossevillii* and *L. borealis* in summer apparently differ at smaller scales (Ford et al. 2002; Grinnell 1918). Reasons for different distributions of the sexes in bats are unclear but may involve limiting competition for resources (Yalden and Morris 1975), differing energy or thermoregulatory needs (Barclay 1991; Thomas 1988), and perhaps additional reproductive and social factors hypothesized to cause sexual segregation in other mammals (Main et al. 1996). Regardless of disparate distributions during summer, both sexes of *L. cinereus* and *L. noctivagans* apparently come together during late summer and early autumn, when copulation in these species may commence. Copulatory activity in *L. cinereus* and *L. noctivagans* likely occurs during autumn and winter (Druecker 1972; Kunz 1982; P. Pyle, pers. comm.; Shump and Shump 1982b), and delayed fertilization may forestall pregnancy until spring (Bouchard et al. 2001; Racey and Entwistle 2000). This relative independence and differential distribution of bat sexes during spring and summer is a unique and understudied phenomenon, with both ecological and management implications.

Among the species studied, it appears that distributions of females change more than those of males, supporting earlier claims that female bats sometimes move farther between winter and summer areas than males (Baker 1978; Constantine 1967; Strelkov 1969). Female bats may need to move farther than males in their search for adequate conditions to give birth and raise young. Reproductive females likely have greater energy and nutritional needs than other bats, as well as more restrictive physiological requirements (Barclay 1989, 1991; Grinevitch et al. 1995; Kunz 1974; Racey and Entwistle 2000; Thomas 1988). In addition, thermal environments in which young bats are raised influence their growth rate and potentially their likelihood of survival (Kunz and Hood 2000). Thus, stringent habitat requirements may force reproductive females to pass up nearer habitats that may be suitable to other bats. Absence of female *L. cinereus* and *L. noctivagans* from mountainous regions of western North America during summer might reflect their inability to raise young under the climatic

conditions and relatively low productivity experienced in these regions. Likewise, it remains to be determined whether abiotic (e.g., climate) or biotic (e.g., competition) forces are influencing the apparent absence of *L. cinereus* and *L. noctivagans* from southeastern United States during the warmer months. Further research into the physiology and energetic needs of these species may help to explain such seasonal distribution patterns.

Records mapped for each species in this study showed some degree of range expansion during late summer and early autumn (August and September). This expansion may be partially the result of breeding activity or population increase after the birth of young, or it may also be associated with exploratory migration, which has been noted in other bats and vertebrate groups (Baker 1978). With the exception of *L. blossevillii*, occurrence records also show that tree bats occur along northern coastlines more during autumn than during spring, which may be associated with coastal navigation. Strelkov (1969) noted bats migrating along coastlines in eastern Europe. The combined effects of coastal and exploratory migration, as well as increase in population size, may account for the fact that the majority of encounters with apparently migratory tree bats occurred during autumn.

In the absence of other methods, mapping museum records is a viable means of formulating hypotheses of seasonal distribution and movement in bats. Because such records are associated with cataloged specimens, materials are available for hypothesis testing using other research techniques, such as stable-isotope analysis (Hobson 1999) and genetic analysis (McCracken et al. 1994). In addition, further research into energetics (e.g., flight costs, foraging, thermoregulation), behavior (e.g., inter- and intraspecific interactions), and habitat use (e.g., roosting needs) of tree bats may help to increase our understanding of their seasonal movements.

Museum data are biased, but they provide a framework on which to refine our understanding of migration in bats. It was beyond the scope of this project to incorporate occurrence records from published and unpublished sources not associated with museum specimens, but future efforts of this kind would undoubtedly benefit by incorporating such data. The importance of consolidating such widely scattered occurrence records and observations was best summarized by one of North America's early naturalists, E. T. Seton (1909:1176) who wrote, "Thus [bats] are being traced on their ronte and marked down in their seasonal homes. Before long the fragmentary observations of many naturalists put together will spell the truth and show us that the Bats are as migratory as the birds, and though long despised, may be also as interesting and beautiful."

Resumen

Aunque existe información bien establecida sobre los patrones migratorios de murciélagos norteamericanos de los géneros *Lasiurus* y *Lasionycteris*, los detalles con respecto a los movimientos estacionales en estas especie son poco conocidos. El objetivo de este estudio es determinar los movimientos estacionales de especies en estos dos generos trazando sus registros de ocurrencia menstual en base a los datos existentes en museos de historia natural. Los cambios mensuales en la distribución de estos registros son una manera indirecta de evaluar los movimientos estacionales de los miembros de estos dos géneros. Durante el invierno, la mayoría de los registros de *Lasiurus cinereus* se concentran en California y México. Durante el verano, la mayoría *L. cinereus* machos se encuentran en el Oeste mientras la mayoría de las hembras ocurren en el Este. *Lasiurus borealis* ocurre en el sureste de Estados Unidos durante invierno, de donde luego se mueve a regiones más septentrionales durante el verano. Contrario a otras regions donde *Lasiurus blossevillii* habita, las colecciones en California sugieren que esta especie es un residente per-

manente del estado. *Lasionycteris noctivagans* muestra también un movimiento de escala continental, aunque en esta especie se pueden diferenciar dos grupos (occidental y oriental). Las distribuciones de cada especie sugieren que no existen movimientos de largo aliento entre Norte y Sud America. Los especimenes de museo son útiles para representar los patrones de movimiento estacional en murciélagos.

Acknowledgments

I extend special thanks to all the museums and museum personnel that helped make this project possible; although they are too numerous to name here, I have attempted to credit, in Appendix I, those who helped. Thanks to M. A. Bogan and J. S. Altenbach for advice and continuous support throughout this project. I am grateful to J. S. Findley, D. M. Armstrong, R. M. Timm, and an anonymous reviewer for providing useful input on earlier drafts of the manuscript. P. Pyle, E. D. Pierson, and W. Gannon kindly provided unpublished information. Thanks to J. Salazar-Bravo for help with Spanish translation. E. Valdez, R. Sherwin, B. Wolf, L. Barker, and A. Hurlbert assisted with various aspects of this research. The Bat Conservation International Student Scholarship Fund, United States Geological Survey Venture Capital Fund, and University of New Mexico Graduate Research Allocation Committee provided partial funding for this project. The manuscript has been submitted in partial fulfillment of requirements for a Ph.D. degree at the University of New Mexico.

Literature Cited

Baker, R. J., J. C. Patton, H. H. Genoways, and J. W. Bickham. 1988. Genic studies of *Lasiurus* (Chiroptera: Vespertilionidae). Occasional Papers, The Museum, Texas Tech University 117:1–15.

Baker, R. R. 1978. The evolutionary ecology of animal migration. Holmes & Meier Publishers, New York.

Baldwin, J. L. 1968. Climatic atlas of the United States. United States Department of Commerce, Environmental Science Services Administration, Environmental Data Service: 1–80.

Barbour, R. W., and W. H. Davis. 1969. Bats of America. University Press of Kentucky, Lexington.

Barclay, R. M. R. 1984. Observations on the migration, ecology and behavior of bats at Delta Marsh, Manitoba. Canadian Field-Naturalist 98:331–336.

Barclay, R. M. R. 1989. The effect of reproductive condition on the foraging behavior of female hoary bats, *Lasiurus cinereus*. Behavioral Ecology and Sociobiology 24:31–37.

Barclay, R. M. R. 1991. Population structure of temperate zone insectivorous bats in relation to foraging behavior and energy demand. Journal of Animal Ecology 60:165–178.

Barclay, R. M. R., P. A. Faure, and D. R. Farr. 1988. Roosting behavior and roost selection by migrating silver-haired bats (*Lasionycteris noctivagans*). Journal of Mammalogy 69:821–825.

Beer, J. R. 1956. A record of a silver-haired bat in a cave. Journal of Mammalogy 37:282.

Bogan, M. A., and P. M. Cryan. 2000. Bats of Wyoming. Pp. 71–94 in Reflections of a naturalist: papers honoring Professor Eugene D. Fleharty (J. R. Choate, ed.). Fort Hays Studies, Special Issue 1.

Bouchard, S., J. Zigouris, and M. B. Fenton. 2001. Autumn mating and likely resorption of an embryo by a hoary bat, *Lasiurus cinereus* (Chiroptera: Vespertilionidae). American Midland Naturalist 145:210–212.

Bradley, R. D., and R. J. Baker. 2001. A test of the genetic species concept: cytochrome-*b* sequences and mammals. Journal of Mammalogy 82:960–973.

Carter, T. D. 1950. On the migration of the red bat, *Lasiurus borealis borealis*. Journal of Mammalogy 31:349–350.

Constantine, D. G. 1959. Ecological observations on lasiurine bats in the North Bay area of California. Journal of Mammalogy 40:13–15.

Constantine, D. G. 1967. Activity patterns of the Mexican free-tailed bat. University of New Mexico Publications in Biology 7:1–79.

Cowan, I. M. 1933. Some notes on the hibernation of *Lasionycteris noctivagans*. Canadian Field-Naturalist 48:74–75.

Crawford, R. L., and W. W. Baker. 1981. Bats killed at a north Florida television tower: a 25-year record. Journal of Mammalogy 62:651–652.

Cryan, P. M., M. A. Bogan, and J. S. Altenbach. 2000. Effect of elevation on distribution of female bats in the Black Hills, South Dakota. Journal of Mammalogy 81:719–725.

Czaplewski, N. J., J. P. Farney, J. K. Jones, Jr., and J. D. Druecker. 1979. Synopsis of bats of Nebraska. Occasional Papers, The Museum, Texas Tech University 61:1–24.

Dalquest, W. W. 1943. Seasonal distribution of the hoary bat along the Pacific Coast. Murrelet 24:21–24.

Davis, W. H., and W. Z. Lidicker, Jr. 1956. Winter range of the red bat, *Lasiurus borealis*. Journal of Mammalogy 37:280–281.

Druecker, J. D. 1972. Aspects of reproduction in *Myotis volans*, *Lasionycteris noctivagans*, and *Lasiurus cinereus*. Ph.D. dissertation, University of New Mexico, Albuquerque.

Findley, J. S., A. H. Harris, D. E. Wilson, and C. Jones. 1975. Mammals of New Mexico. University of New Mexico Press, Albuquerque.

Findley, J. S., and C. Jones. 1964. Seasonal distribution of the hoary bat. Journal of Mammalogy 45:461–470.

Ford, W. M., M. A. Menzel, J. M. Menzel, and D.

J. WELCH 2002. Influence of summer temperature on sex ratios in eastern red bats (*Lasiurus borealis*). American Midland Naturalist 147:179–184.

GENOUD, M. 1993. Temperature regulation in subtropical tree bats. Comparative Biochemistry and Physiology. A. Comparative Physiology 104:321–331.

GENOWAYS, H. H., AND R. J. BAKER. 1988. *Lasiurus blossevillii* (Chiroptera: Vespertilionidae) in Texas. Texas Journal of Science 40:111–113.

GOSLING, N. M. 1977. Winter record of silver-haired bat, *Lasionycteris noctivagans* (Le-Conte), in Michigan. Journal of Mammalogy 58:657.

GRIFFIN, D. R. 1970. Migration and homing of bats. Pp. 233–264 in Biology of bats (W. A. Wimsatt, ed.). Academic Press, New York.

GRINEVITCH, L., S. L. HOLROYD, AND R. M. R. BARCLAY. 1995. Sex difference in the use of daily torpor and foraging time by big brown bats. Journal of Zoology (London) 235:301–309.

GRINNELL, H. W. 1918. A synopsis of the bats of California. University of California Publications in Zoology 17:223–404.

HAFNER, M. S., W. L. GANNON, J. SALAZAR-BRAVO, AND S. T. ALVAREZ-CASTAÑEDA. 1997. Mammal collections of the western hemisphere: a survey and directory of existing collections. American Society of Mammalogists, Lawrence, Kansas.

HALL, E. R. 1946. Mammals of Nevada. University of California Press, Berkeley.

HALL, E. R. 1981. The mammals of North America. John Wiley & Sons, Inc., New York 1:1–600 + 90.

HAYMAN, R. W. 1959. American bats reported in Iceland. Journal of Mammalogy 40:245–246.

HILL, J. E., AND D. W. YALDEN. 1990. The status of the hoary bat (*Lasiurus cinereus*) as a British species. Journal of Zoology (London) 222:694–697.

HITCHCOCK, H. B. 1943. Hoary bat, *Lasiurus cinereus*, at Southampton Island, N. W. T. Canadian Field-Naturalist 57:86.

HOBSON, K. A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120:314–326.

HOFFMEISTER, D. F. 1970. The seasonal distribution of bats in Arizona: a case for improving mammalian range maps. Southwestern Naturalist 15:11–22.

HOWELL, A. H. 1908. Notes on diurnal migrations of bats. Proceedings of the Biological Society of Washington 21:35–38.

IZOR, R. J. 1979. Winter range of the silver-haired bat. Journal of Mammalogy 60:641–643.

JACKSON, H. H. T. 1961. Mammals of Wisconsin. University of Wisconsin Press, Madison.

JONES, J. K., JR., E. D. FLEHARTY, AND P. B. DUNNIGAN. 1967. The distributional status of bats in Kansas. Miscellaneous Publications, Museum of Natural History, University of Kansas 46:1–33.

JONES, J. K., JR., R. P. LAMPE, C. A. SPENRATH, AND T. H. KUNZ. 1973. Notes on the distribution and natural history of bats in southeastern Montana. Occasional Papers, The Museum, Texas Tech University 15:1–12.

JONES, J. M. 1884. The mammals of Bermuda. United States National Museum Bulletin 25:143–161.

KUNZ, T. H. 1971. Reproduction of some vespertiliomid bats in central Iowa. American Midland Naturalist 86:477–486.

KUNZ, T. H. 1974. Feeding ecology of a temperate insectivorous bat (*Myotis velifer*). Ecology 55:693–711.

KUNZ, T. H. 1982. *Lasionycteris noctivagans*. Mammalian Species 172.1–5.

KUNZ, T. H., AND W. R. HOOD. 2000. Parental care and postnatal growth in the Chiroptera. Pp. 415–468 in Reproductive biology of bats (E. G. Crichton and P. H. Krutzsch, eds.). Academic Press, San Diego, California.

LAVAL, R. K., AND M. L. LAVAL. 1979. Notes on reproduction, behavior, and abundance of the red bat, *Lasiurus borealis*. Journal of Mammalogy 60:209–212.

LINSLEY, J. H. 1842. A catalogue of the Mammalia of Connecticut, arranged according to their natural families: furnished for the Yale Natural History Society. American Journal of Science and Arts 43:345–354.

MACKIEWICZ, J., AND R. H. BACKUS. 1956. Oceanic records of *Lasionycteris noctivagans* and *Lasiurus borealis*. Journal of Mammalogy 37:442–443.

MAIN, M. B., F. W. WECKERLY, AND V. C. BLEICH. 1996. Sexual segregation in ungulates: new directions for research. Journal of Mammalogy 77:449–461.

MAUNDER, J. E. 1988. First Newfoundland record of the hoary bat, *Lasiurus cinereus*, with a discussion of other records of migratory tree bats in Atlantic Canada. Canadian Field-Naturalist 102:726–728.

MCCRACKEN, G. F., M. K. MCCRACKEN, AND A. T. VAWTER. 1994. Genetic structure in migratory populations of the bat *Tadarida braviliensis mexicana*. Journal of Mammalogy 75:500–514.

MEARNS, E. A. 1898. A study of the vertebrate fauna of the Hudson Highlands, with observations on the Mollusca, Crustacea, Lepidoptera, and the flora of the region. Bulletin of the American Museum of Natural History 10:303–352.

MERRIAM, C. H. 1887. Do any Canadian bats migrate? Evidence in the affirmative. Transactions of the Royal Society of Canada 4:85–87.

MILLER, G. S., JR. 1897. Migration of bats on Cape Cod, Massachusetts. Science 5:541–543.

MORALES, J. C., AND J. W. BICKHAM. 1995. Molecular systematics of the genus *Lasiurus* (Chiroptera: Vespertilionidae) based on restriction-site maps of the mitochondrial ribosomal genes. Journal of Mammalogy 76:730–749.

MUMFORD, R. E. 1963. A concentration of hoary bats in Arizona. Journal of Mammalogy 44:272.

NAGORSEN, D. W., A. A. BRYANT, D. KERRIDGE, G. ROBERTS, A. ROBERTS, AND M. I. SARELL. 1993. Winter bat records for British Columbia. Northwestern Naturalist 74:61–66.

NORTON, A. H. 1930. A red bat at sea. Journal of Mammalogy 11:225–226.

ORR, R. T. 1950. Notes on the seasonal occurrence of red bats in San Francisco. Journal of Mammalogy 31:457–458.

PADGETT, T. M., AND R. K. ROSE. 1991. Bats (Chiroptera: Vespertilionidae) of the Great Dismal Swamp

of Virginia and North Carolina. Brimleyana 17:17–25.

PETERSON, R. L. 1970. Another red bat, *Lasiurus borealis*, taken aboard ship off the coast of Nova Scotia. Canadian Field-Naturalist 84:401.

POLACO, O. J., J. ARROYO-CABRALES, AND J. K. JONES, JR. 1992. Noteworthy records of some bats from Mexico. Texas Journal of Science 44:331–338.

RACEY, P. A., AND A. C. ENTWISTLE. 2000. Life-history and reproductive strategies of bats. Pp. 363–414 in Reproductive biology of bats (E. G. Crichton and P. H. Krutzsch, eds.). Academic Press, San Diego, California.

RAMÍREZ-PULIDO, J., AND A. CASTRO-CAMPILLO. 1994. Bibliografía reciente de los mamíferos de México 1989–1993. Universidad Autónoma Metropolitana, Mexico City, Mexico.

RHODES, S. N. 1903. The mammals of Pennsylvania and New Jersey. Privately published, Philadelphia, Pennsylvania.

SAUNDERS, W. E. 1930. Bats in migration. Journal of Mammalogy 11:225.

SCHOWALTER, D. B., W. J. DORWARD, AND J. R. GUNSON. 1978. Seasonal occurrence of silver-haired bats (*Lasionycteris noctivagans*) in Alberta and British Columbia. Canadian Field-Naturalist 92:288–291.

SETON, E. T. 1909. Life-histories of northern animals: an account of the mammals of Manitoba. Charles Scribner's Sons, New York.

SHUMP, K. A., JR., AND A. U. SHUMP. 1982a. *Lasiurus borealis*. Mammalian Species 183:1–6.

SHUMP, K. A., JR., AND A. U. SHUMP. 1982b. *Lasiurus cinereus*. Mammalian Species 185:1–5.

SPARKS, D. W., AND J. R. CHOATE. 2000. Distribution, natural history, conservation status, and biogeography of bats in Kansas. Pp. 173–228 in Reflections of a naturalist: papers honoring Professor Eugene D. Fleharty (J. R. Choate, ed.). Fort Hays Studies, Special Issue 1.

STRELKOV, P. P. 1969. Migratory and stationary bats (*Chiroptera*) of the European part of the Soviet Union. Acta Zoologica Cracoviensia 14:393–436.

SZEWCZAK, J. M., S. M. SZEWCZAK, M. L. MORRISON, AND L. S. HALL. 1998. Bats of the White and Inyo Mountains of California-Nevada. Great Basin Naturalist 58:66–75.

TENAZA, R. R. 1966. Migration of hoary bats on South Farallon Island, California. Journal of Mammalogy 47:533–535.

TERRES, J. K. 1956. Migration records of the red bat, *Lasiurus borealis*. Journal of Mammalogy 37:442.

THOMAS, D. W. 1988. The distribution of bats in different ages of Douglas-fir forests. Journal of Wildlife Management 52:619–626.

THOMAS, O. 1921. Bats on migration. Journal of Mammalogy 2:167.

TIMM, R. M. 1989. Migration and molt patterns of red bats, *Lasiurus borealis* (Chiroptera: Vespertilionidae) in Illinois. Bulletin of the Chicago Academy of Sciences 14:1–7.

TURNER, R. W. 1974. Mammals of the Black Hills of South Dakota and Wyoming. Miscellaneous Publications, Museum of Natural History, University of Kansas 60:1–178.

TYLER, J. D., AND L. PAYNE. 1982. Second Oklahoma record for the silver-haired bat, *Lasionycteris noctivagans*. Southwestern Naturalist 27:245.

USINGER, R. L. 1966. Monograph of Cimicidae. Thomas Say Foundation, Entomological Society of America, College Park, Maryland.

VALDEZ, E. W., J. N. STUART, AND M. A. BOGAN. 1999. Additional records of bats from the Middle Rio Grande Valley, New Mexico. Southwestern Naturalist 44:398–400.

VAN GELDER, R. G., AND D. B. WINGATE. 1961. The taxonomy and status of bats in Bermuda. American Museum Novitates 2029:1–9.

VAUGHAN, T. A. 1953. Unusual concentration of hoary bats. Journal of Mammalogy 34:256.

VAUGHAN, T. A., AND P. H. KRUTZSCH. 1954. Seasonal distribution of the hoary bat in southern California. Journal of Mammalogy 35:431–432.

WATKINS, L. C., J. K. JONES, JR., AND H. H. GENOWAYS. 1972. Bats of Jalisco, México. Special Publications, The Museum, Texas Tech University 1:1–44.

WHITAKER, J. O., JR., AND W. J. HAMILTON, JR. 1998. Mammals of the eastern United States. 3rd ed. Comstock Publishing Associates, Ithaca, New York.

YALDEN, D. W., AND P. A. MORRIS. 1975. The lives of bats. The New York Times Book Co., New York.

YATES, T. L., D. J. SCHMIDLY, AND K. L. CULBERTSON. 1976. Silver-haired bat in Mexico. Journal of Mammalogy 57:205.

ZINN, T. L., AND W. W. BAKER. 1979. Seasonal migration of the hoary bat, *Lasiurus cinereus*, through Florida. Journal of Mammalogy 60:634–635.

Submitted 1 April 2002. Accepted 31 July 2002.

Associate Editor was Thomas J. O'Shea.

APPENDIX I

Following is a list of museums and museum personnel that contributed data on tree bats from their collections. Unless otherwise noted, museum acronyms follow those listed in Hafner et al. (1997). ACUNHC, T. E. Lee, Jr.; AMNH, T. Pacheco; ANSP, N. Gilmore; APM, R. D. Strickland; ASNHC, R. Dowler; BMNHC, B. Williams; BSNS, A. R. Clark; CACA, D. Kayser; CCVC, A. B. McPherson; CCW, D. Crowe; CLNP, M. Merryman-B.; CM-MVUP, V. Tejera-N.; CMN, M. Gosselin, D. Balkwill; CM-UMSNH, A. Núñez-G.; CSUF, C. Kronberg, J. Hogue; CSULB, D. Huckaby; CUMZ, J. Tyler; CUSC, S. Miller; CUVC, C. Dardia; DEVA, B. Davenport; DIX, A. Barnhum; DMNH, H. Coovert; DMNHI, L. Skibinski; EBRG, J. Sanchez-H.; ENCB, T. Alvarez-S., N. Gonzalez-R., N. Sanchez-C.; FLC, J. Ortega; FMNH, W. Stanley, L. Heaney; GBNM, W. Howell; GRSM, D. DeFoe; HCMZ, K. Winnett-M.; HCNHSC, R. Glotzhober; HMNZ, T. Sordahl; HSU, T. Lawlor, P. Holahan; IBUNAM, F. Cervantes, J. Vargas-

Q.; IEEUACH, M. Gallardo, F. Mondaca-L.; INHS, L. Page; IOWA, G. Schrimper, C. Optiz; JMM, J. Iverson; KU, T. Holmes, R. Timm; LSUMZ, M. Hafner; MBUCV, R. Perez-H.; MCZ, M. Rutzmoser; MECN, I. Castro; MHP, J. Choate; MN Biol. Surv., G. Nordquist; MLP, D. Verzi; MLZ, J. Hafner; MMNH, A. Brunet; MMNS, S. Peyton; MMP, D. Romero; MSU, L. Abraczinskas, B. Lundrigan, MSUMC, T. Derting, MU, P. Daniel; MUSM, E. Vivar, V. Pacheco; MVZ, J. Patton; MWSU, F. Stangl, Jr.; NBM, D. McAlpine; NCSM, M. K. Clark, L. Gatens; NDUS, W. Bleier; NEMSU, S. Burt; NMMNH, D. Hafner, J. McConachie; NSMC, G. Baumgardner; NZCS, P. Ouboter, S. Sahdew; OMNH, J. Braun; OSU, S. Hoofer, A. Echelle; OSUFW, D. Markle, B. Coblentz; PGMNH, P. M. Finnegan; PM, E. Webb, J. Hall; PMA, W. Weimann; PMNH, L. Thomas; PMS, J. Winchell; PSU, R. Forbes, A. Cramer; PWRC, M. Perry; QCAZ, L. Coloma, P. Jarrin-V.; RBCM, D. Nagorsen; ROM, S. Woodward; RPPMC, S. Dobbyn, R. Hart; SBMNH, P. Collins; SDAKS, S. Pederson; SDNHM, P. Unitt; SDSU, M. Van Patten; SETON, S. Zimmer; SIUCM, G. Feldhamer; SJUBC, P. Chu; SM, D. Lintz; SMM, F. Jannett, Jr.; SRSU, J. Mueller; SUVM, G. Paulson; TCWC, R. Honeycutt, D. Schlitter; TMM, E. Lundelius, P. Owen, L. Ernest; TTU, R. Monk, R. J. Baker; UA, Y. Petryszyn, M. Bucci, UAFMZ, N. Glover-M., UAM, D. McDonald; UAMZ, W. Roberts; UBC, C. Adkins; UCLA, F. Hertel; UCM, R. Humphrey; UDEL, N. Nazdrowicz; UGAMNH, E. Reitz, E. McGee, UGDZ, G. Nacekivell; UID, A. D. Johnson; UIMNH, J. Hoffmann, C. Mayer; UMA, K. Doyle; UMMZ, P. Myers, S. Hinshaw; UMNH, E. Rickart; UMZM, D. Dyer; UND, R. Seabloom; UNH, M. Pellissier-S.; UNK, J. Springer; UNM, C. Ramotnik, W. Gannon; UNO, K. Geluso; UNSM, P. Freeman, T. Labedz; UOMNH, P. Endzweig; USI, J. Bandoli; USNM, R. Fisher, C. Ludwig; UTA, J. A. Campbell, L. Ammerman; UTEP, A. Harris; UWBM, G. Kenagy, A. Schwandt-A.; UWSP, C. Long; VCU, J. Pagels, M. Hackett; WCW, C. Drabek; WSC, D. Lovejoy; WSU, S. Zeveloff, C. Harris-F.; WVMS, M. E. Hight; WWF, S. Glasscock; YNP, B. Beroza.