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Saccopteryx bilineata.

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Saccopteryx Illiger, 1811

Saccopteryx Illiger, 1811:121; type species *Vespertilio leptura* Schreber, 1774, by monotypy.

Urocryptus Temminck, 1838:31; type species *Urocryptus bilineatus* Temminck, 1838, by monotypy.

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Emballonuridae, Subfamily Emballonurinae. The genus includes four species, *S. bilineata*, *S. canescens*, *S. gymnura*, and *S. leptura* (Koopman, 1993). The following key to the species is modified from Eisenberg (1989), Jones and Hood (1993), Linares (1986), and Sanborn (1937).

1 Attachment of wing membrane to tibia; two longitudinal white stripes on dorsum 2
Attachment of wing membrane to metatarsals; no longitudinal stripes on dorsum .... *S. gymnura*
2 Dorsal pelage tawny or chocolate brown; membranes brown; length of head and body <45 mm; forearm <43 mm 3
Dorsal pelage blackish; membranes blackish; length of head and body >45 mm; length of forearm >43 mm .... *S. bilineata*
3 Dorsal pelage brown, slightly burnished; longitudinal lines usually distinct; hind foot >8 mm .... *S. leptura*
Dorsal pelage grizzled or slightly frosted with gray or yellow, especially on head; white longitudinal lines may be indistinct; hind foot <8 mm .... *S. canescens*

Saccopteryx bilineata (Temminck, 1838)

Greater White-lined Bat

Urocryptus bilineatus Temminck, 1838:33. Type locality "Suriname."

E[mballonura] insignis Wagner, 1855:695. Type locality "Brazil."

Saccopteryx bilineata, Peters, 1867:471. First use of current name combination.

Saccopteryx perspicillifer Miller, 1899:176. Type locality "Caura, Trinidad."

CONTEXT AND CONTENT. As for the genus. Bats from Mexico and Central America have been referred to *S. b. centralis* Thomas, 1904 (Alvarez, 1968). Jones and Hood (1993) considered *S. b. perspicillifer* to be synonymous with *S. b. bilineata*, which also includes *S. b. centralis*. Currently, *S. bilineata* is regarded as monotypic (Hall, 1981).

DIAGNOSIS. *Saccopteryx bilineata* is a dark, small to medium-sized bat (Fig. 1). Two whitish longitudinal stripes on the dorsum distinguish this species from other superficially similar bats (e.g., *Balantiopteryx*, *Peropteryx*, *Centronycteris*, *Cormura*, and *S. gymnura*—Sanborn, 1937). However, *Rhynchonycteris naso* and other species of *Saccopteryx* possess similar markings, and often are sympatric with *S. bilineata*. The proboscis bat (*Rhynchonycteris naso*) can be distinguished from *S. bilineata* by its smaller size, long snout, grizzled, paler dorsal coloration, and the presence of small tufts of grayish hair on the forearms (Eisenberg, 1989; Jones and Hood, 1993). In addition, all members of the genus *Saccopteryx* possess wing sacs, which are absent in *Rhynchonycteris* (Sanborn, 1937). Several characters distinguish *S. bilineata* from *S. canescens*. *S. bilineata* has more distinct dorsal stripes (Eisenberg, 1989; Linares, 1986), length of head and body >45 mm (Eisenberg, 1989), and length of forearm >43 mm (Jones and Hood, 1993). *S. canescens* has fainter stripes, length of head and <45 mm (Eisenberg, 1989), and length of forearm <43 mm (Jones and Hood, 1993). In addition, there may be habitat differences associated with these two species (Handley, 1976). *S. leptura* also resembles *S. bilineata*, with which it is sympatric over much of its range. However, *S. leptura* is smaller (head and body length <45 mm and length of forearm <43 mm—Eisenberg, 1989; Jones and Hood, 1993). Moreover, the dorsal pelage of *S. bilineata* usually is blackish, whereas it is brown in *S. leptura* (Jones and Hood, 1993; Linares, 1986; Sanborn, 1937).

GENERAL CHARACTERS. The upper parts of *S. bilineata* are black when the bat is in fresh pelage, but grade to deep brown whenever pelage becomes worn. Two wavy lines of whitish hairs extend from the shoulders onto the rump. Underparts are brownish to gray in color. The uropatagium is thinly haired to the exsertion of the tail. The skull (Fig. 2) has well-developed postorbital processes, and it has premaxillaries that usually are free, always incomplete, with their boundaries clearly outlined. The humerus has a well-developed trochanter and a capitellum that is nearly in line with the shaft. The second digit of the manus has a metacarpal but no phalanges. The seventh cervical vertebra is not fused to the pectoral girdle. The tail perforates the upper surface of the interfemoral membrane. The muzzle is simple, lacks a leaflike excrescence, and the distal part of the rostrum is without dorsal inflations (Hall, 1981).

Saccopteryx bilineata males are smaller than females, and possess a large glandular sac in the antebrachial membrane used in social displays (Bradbury and Emmons, 1974; Bradbury and Vehrencamp, 1976*a*). Average external measurements (in mm) of males and females, respectively, from Venezuela are as follows: total length, 73.88 ($n = 24$), 76.00 ($n = 42$); length of tail, 21.58 ($n = 24$), 21.58 ($n = 43$); length of ear, 17.96 ($n = 24$), 17.51 ($n = 43$); length of hind foot, 12.25 ($n = 24$), 12.11 ($n = 43$); length of forearm, 47.13 ($n = 27$), 49.16 ($n = 42$). Body mass ranges from 8.5 to 9.3 g with females weighing slightly more than males (Eisenberg, 1989). Ranges of cranial measurements (in mm) are, condylobasal length, 13.2–15.7 and length of upper toothrow, 5.8–7.4 (Hall, 1981). The dental formula is i 1/3, c 1/1, p 2/2, m 3/3, total 32 (Eisenberg, 1989; Hall, 1981).

DISTRIBUTION. The geographic range of this species (Fig. 3) extends from Jalisco and Veracruz, Mexico, the Guianas, Trinidad, Tobago, south to Bolivia and eastern Brazil, and thence southward to Rio de Janeiro, Brazil (Koopman, 1993). No fossils are known for this species.

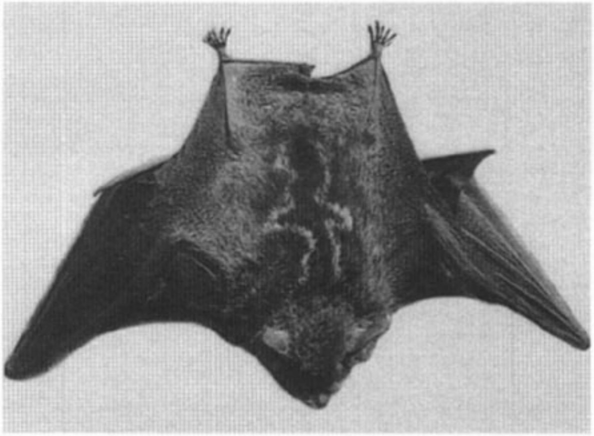

FIG. 1. Photograph of *Saccopteryx bilineata*. Photograph by Peter V. August.

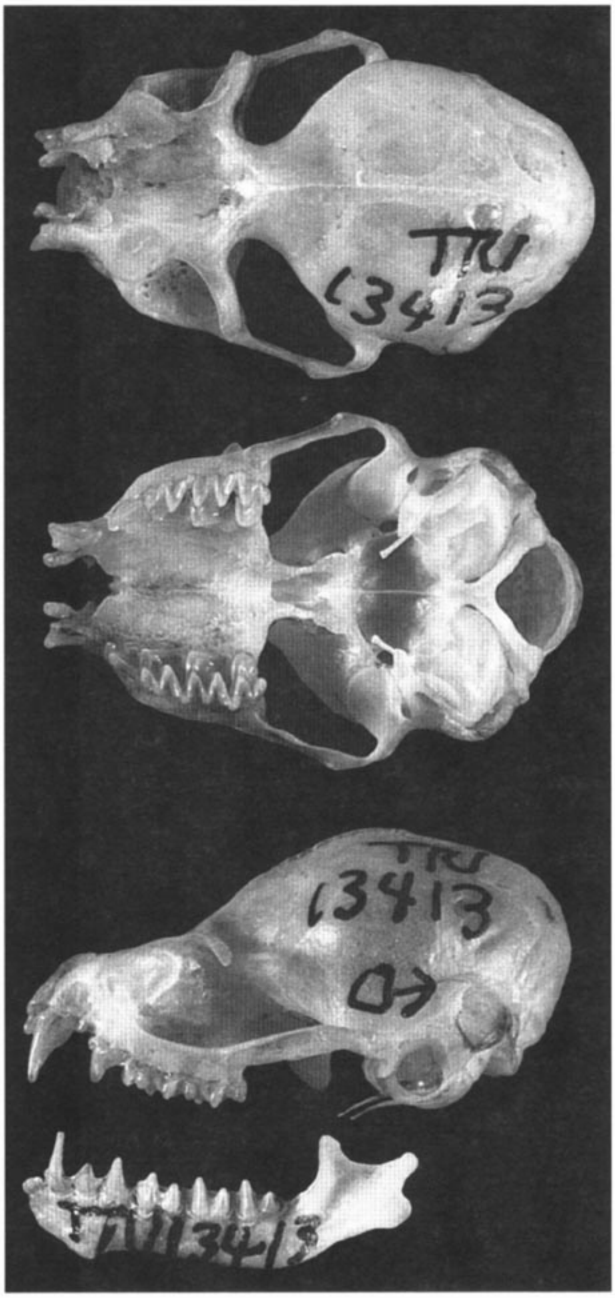

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of a male *Saccopteryx bilineata* from 23 miles N San Pedro Sula, Cortez, Honduras (Texas Tech University 13413). Greatest length of cranium is 15.9 mm.

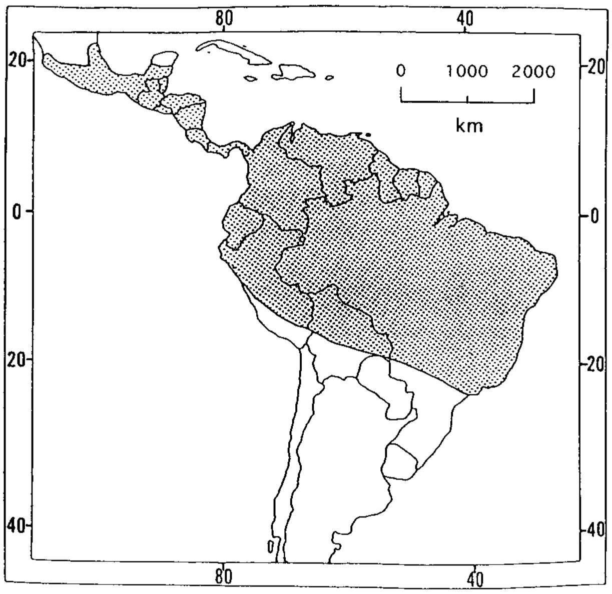

FIG. 3. Geographic distribution of *Saccopteryx bilineata* (Hall, 1981; Jones and Hood, 1993; Polanco et al., 1992).

FORM AND FUNCTION. *Saccopteryx bilineata* is capable of maintaining appreciable temperature differentials with the environment. It usually remains normothermic and is alert and active at daytime roosting sites. This bat has a basal metabolic rate of ca. $1.86 \pm 0.55\ \text{cm}^3\ \text{O}_2\ \text{g}^{-1}\ \text{h}^{-1}$ (Genoud and Bonaccorso, 1986), which is considered high for an insectivorous bat (McNab, 1982, 1989). This high metabolism may be in response to the abundance and seasonal stability of the prey species of this bat (Genoud and Bonaccorso, 1986). Five out of nine individuals taken in Trinidad during August were molting (Carter et al., 1981).

As is typical of insectivorous bats, the greater white-lined bat utilizes echolocation to pursue and capture prey. Search-phase emissions of *S. bilineata* are relatively long in duration and occur in pairs. They are characterized by a slight rise in frequency at the onset of the pulse, followed by a long, constant frequency portion, and terminated with a slight decrease in frequency (Barclay, 1983; Bradbury and Vehrencamp, 1976*a*). The first call of the search-phase pair lasts approximately 5.1–6.7 ms (Barclay, 1983). Frequency ranges are 47–50 kHz for populations from Costa Rica (Bradbury and Vehrencamp, 1976*a*), ca. 42–46 kHz for bats from Panama (Barclay, 1983), and ca. 43–45 kHz for individuals from Belize (O'Farrell and Miller, 1997). This type of shift in emission frequencies used by different populations of *S. bilineata* also was noted by Pye (1973). The second of the search calls occurs 48–58 ms after the first. This call is similar to the first, but has a duration of 4.8–6.0 ms (Barclay, 1983; Bradbury and Vehrencamp, 1976*a*). In Costa Rica and Panama, the second of the paired calls reportedly has frequencies 2–3 kHz lower than the first (Barclay, 1983; Bradbury and Vehrencamp, 1976*a*), whereas in Belize, the second call is about 3 kHz higher than the first (O'Farrell and Miller, 1997). The majority of these search-phase calls is emitted in the second harmonic (Barclay, 1983; Bradbury and Vehrencamp, 1976*a*). During the approach or pursuit phase, the calls become shorter with a more pronounced rise in frequency than in the search phase. Terminal-stage emissions, or feeding buzzes, are shorter yet (ca. 1.0–1.7 ms) and are characterized by a less pronounced rise in frequency. These calls primarily are descending-frequency signals (Barclay, 1983). The frequency/time display of a vocal sequence of *S. bilineata* from Belize is presented in Fig. 4.

ONTOGENY AND REPRODUCTION. The reproductive season of the greater white-lined bat is synchronized in Trinidad, with females producing a single young from late May to mid-June (Bradbury and Vehrencamp, 1976*a*; Nowak, 1991). Parturition occurs at the onset of the rainy season (Bradbury and Vehrencamp, 1976*a*). Thus, gestation occurs mostly during periods of low food availability (the dry season). Birth takes place as the food supply begins to rise, and juvenile development occurs in concert with maximum food levels (Bradbury and Vehrencamp, 1977*b*). Each year, 17% of females fail to give birth, probably in response to food stress (Bradbury and Vehrencamp, 1976*b*, 1977*b*).

Females do not leave young at daytime roosts, but carry them during foraging (Bradbury and Vehrencamp, 1976*a*, 1977*b*) or leave them at a night roost (usually in a tree) for the night (Nowak, 1991). Young bats can fly at ca. 2 weeks of age. They are weaned at 10–12 weeks, and at this time, nearly all yearling females disperse to other sites. Age of first parturition is one year. Young males may remain near their parents and await the opportunity to take over a harem or obtain a group of females for their own harems (Bradbury and Emmons, 1974; Bradbury and Vehrencamp, 1976*a*; Nowak, 1991).

Pregnant females have been recorded in April in Jalisco, Mexico (Watkins et al., 1972); March, April, and May in Belize and Guatemala (Rick, 1968); February in the Yucatan Peninsula (Jones et al., 1973); March in El Salvador (LaVal and Fitch, 1977); March,

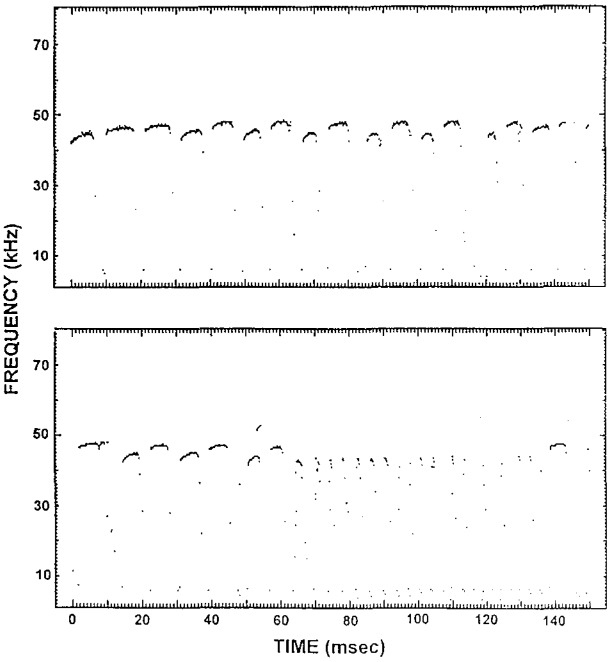

FIG. 4. Frequency/time display of a vocal sequence of *Saccopteryx bilineata* from Belize. Top display begins with orientation/search calls and merges into pursuit calls. Bottom display is a continuation of the same sequence and terminates with a feeding buzz (adapted from O'Farrell and Miller, 1997).

April, May, September, and December in Costa Rica (LaVal and Fitch, 1977); and January, February, March, and April in Panama (Fleming et al., 1972). Lactating females were noted in Trinidad during August (Carter et al., 1981). These data seem to indicate an extended breeding period for *S. bilineata* over parts of its range. Nonpregnant females have been obtained in the months of June, July, and August (Carter et al., 1981; Fleming et al., 1972; Tuttle, 1970). Two males taken on 7 August had testes measuring 2 and 3 mm in length (Carter et al., 1981).

ECOLOGY. The greater white-lined bat is a common resident of buildings and other structures throughout its range (Polanco et al., 1992; Rick, 1968). *S. bilineata* also roosts in well-lighted caves, among trees and other vegetation, and under bridges (Goodwin and Greenhall, 1961), and may utilize ruins as daytime roosts (Polanco et al., 1992; Rick, 1968). This species also has been discovered roosting in trees during the daytime in Veracruz, Mexico (Hall and Dalquest, 1963), Ecuador (Webster and Jones, 1984), Costa Rica, and Trinidad (Bradbury and Vehrencamp, 1976*a*). In addition, *S. bilineata* has been observed at entrances of apertures in the face of limestone cliffs in Veracruz, Mexico (Hall and Dalquest, 1963). In Costa Rica, colonies of *S. bilineata* were found in a well-illuminated area on the walls of a cave housing *Balantiopteryx plicata* (Bradbury and Vehrencamp, 1976*a*). All individuals of *S. bilineata* noted by Anderson et al. (1982) in Bolivia were near a source of water in, or close to, tropical forests. All of these bats were taken at low elevations, whereas in Columbia, Hershkovitz (1949) found this species to occupy montane slopes as well.

Other species of bats known to roost with *S. bilineata* include *Balantiopteryx plicata* (Bradbury and Vehrencamp, 1976*a*), *Saccopteryx leptura, Peropteryx macrotis, Noctilio leporinus, Micronycteris hirsuta, M. megalotis, M. nicefori, M. sylvestris, Phyllostomus discolor, P. hastatus, Trachops cirrhosus, Glossophaga soricina, Carollia perspicillata, Artibeus jamaicensis, A. lituratus, Uroderma bilobatum, Desmodus rotundus,* and *Diaemus youngi* (Goodwin and Greenhall, 1961). When encountered with *N. leporinus, D. rotundus,* or *D. youngi, S. bilineata* often is found roosting at lower elevations, usually close to the entrance of a cave or hollow tree (Goodwin and Greenhall, 1961).

Greater white-lined bats may form colonies of up to 50 individuals, but rarely does a colony consist of more than 15 bats (Goodwin and Greenhall, 1961). The mean sizes of two colonies of *S. bilineata* in Costa Rica were 5.5 and 6.3 individuals, whereas the mean colony size on Trinidad was 8.1. Some colonies from Costa Rica and Trinidad have been reported to harbor as many as 50 individuals (Bradbury and Vehrencamp, 1976*a*). In Costa Rica, colonies are spaced an average of 60 m apart (Bradbury and Vehrencamp, 1976*b*). In Costa Rica and Trinidad, females comprise 62% of the adult population. Colony size is bimodal in Costa Rica and Trinidad, with colonies either being small or large, with few intermediate in size. Heterogeneity in colony size is not due to relocation of individual bats or seasonal changes (Bradbury and Vehrencamp, 1976*a*).

Population densities of 0.7 bats/ha have been recorded for *S. bilineata* on Trinidad and Costa Rica (Bradbury and Vehrencamp, 1976*a*). In these areas, the biomass density of *S. bilineata* was estimated at 6 g/ha (Bradbury and Vehrencamp, 1977*a*). Population densities of *S. bilineata* are determined, to some degree, by available food resources within an area. Colonies of *S. bilineata* were found to forage through an area of ca. 6–18 ha, depending upon area location and season of the year. Foraging areas and colony roosting sites are moved throughout an area as bats take advantage of shifting insect abundance in deciduous woodland habitat (Bradbury and Vehrencamp, 1976*a*).

Saccopteryx bilineata is a strict insectivore (Bradbury and Vehrencamp, 1976*a*; Fleming et al., 1972). Where the greater white-lined bat is sympatric with *R. naso,* it takes larger insect prey items. When it forages with *Balantiopteryx plicata* in Costa Rica, the greater white-lined bat maintains a strict habitat separation (Bradbury and Vehrencamp, 1976*a*). *S. bilineata* feeds upon coleopterans and dipterans in Costa Rica and Trinidad. Insects are taken in direct proportion to their availability around the vegetation over which the bats are foraging. Although lepidopterans frequently are consumed by *S. bilineata,* specialization upon a particular type of prey is not known to occur with this bat (Bradbury and Vehrencamp, 1976*a*).

In Belize, *S. bilineata* begins foraging slightly later than its congener, *S. leptura* (McCarthy, 1987). In Peru, *S. bilineata* is one of the earliest emerging foragers (Tuttle, 1970). In Costa Rica, *S. bilineata* has been observed chasing the smaller *S. leptura* from feeding grounds at dusk (Bradbury and Vehrencamp, 1976*a*). In Costa Rica, *S. bilineata* and *S. leptura* forage in the same habitat without altitudinal segregation. *Rhynchonycteris naso* and *S. bilineata* share the same foraging habitat during at least part of the year where the two species are sympatric. The greater white-lined bat has been reported to be a solitary forager (Bradbury and Vehrencamp, 1976*a*). *S. bilineata* will sit out a heavy nocturnal rain at a night roost, thus limiting its foraging time for the evening (Bradbury and Vehrencamp, 1976*b*).

Foraging flights of *S. bilineata* are a mixture of straight-line chasing in open sites at 3–8 m above the ground and sharp turns within 1–5 m of an obstruction. *S. bilineata* flies at speeds averaging 5.75 m/sec (Morrison, 1980). Foraging is conducted within a beat for 20–30 minutes before the bat moves to an adjacent beat, although some bats may forage around trees for many minutes. After two or three hours of foraging, *S. bilineata* leaves its foraging beat to roost in a nearby tree. Nearly all foraging is conducted over and around vegetation, and foraging sites are positively correlated with phenacology in an area (Bradbury and Vehrencamp, 1976*a*). The food supply of *S. bilineata* is highly seasonal (Bradbury and Vehrencamp, 1977*b*) due to temporal variations in prey densities, and individuals must utilize new foraging patches about every 5–10 weeks (Bradbury and Vehrencamp, 1976*b*).

Ectoparasites known to infest *S. bilineata* include *Euctenodes* (Streblidae), *Eutrombicula göldii, Trombicula saccopteryx,* and *T. vesperuginis* (Trombiculidae—Goodwin and Greenhall, 1961). In amazonian Peru, the greater white-lined bat harbors the tapeworm, *Hymenolepis mazanensis.* This cestode also infects *R. naso* from the same geographic locality (Vaucher, 1986). All individuals examined for rabies during a study of *S. bilineata* from Trinadad were negative for the virus. Histoplasmosis capsulatum has been detected at sites where *S. bilineata* roosts in association with *Desmodus rotundus* (Goodwin and Greenhall, 1961).

BEHAVIOR. The greater white-lined bat usually roosts in groups, although males often are solitary (Bradbury and Vehrencamp, 1976*a*). Temporary harems usually are formed (Bradbury and Vehrencamp, 1977*a*), but as many as 62% of males were found to be solitary, peripheral bachelors in Panama (Tannenbaum, 1975).

Also, males may roost separately from females, and adult females do not move between different colonies (Bradbury and Emmons, 1974; Bradbury and Vehrencamp, 1976*a*).

Harems of a colony roost together in a single tree, but each harem male defends an area of ca. 1–3 m^2 of vertical roost space. Territorial defense and competition for territories and females is conducted by males throughout the year (Nowak, 1991). Females within a harem are aggressive toward newcomers, but no aggression has been noted by harem males toward new females. In general, there is a close correlation between day-roost group membership and the location of nocturnal foraging sites within an area (Bradbury and Vehrencamp, 1976*a*).

Saccopteryx bilineata maintains colony-specific annual foraging ranges that are defended against not only conspecifics from other colonies, but also against intrusion by adult males of the same colony (Bradbury and Vehrencamp, 1976*a*, 1977*a*). All members of a given colony forage within a common site at any given time. The colony foraging site is partitioned into individual harem territories defended by harem males containing the individual beats of all current harem females. Harem females forage adjacent to each other in multiple beats of 10–20 m in length, and the harem male's foraging territory overlaps those of his females. Harems usually consist of an adult male and up to eight adult females. Males obtain harems either by splitting an existing harem or by replacing a harem male that has been lost (Bradbury and Vehrencamp, 1976*a*).

GENETICS. *Saccopteryx bilineata* has 2n = 26 chromosomes and FN = 36. The X and Y chromosomes are acrocentric (Baker and Jordan, 1970; Baker et al., 1992; Hood and Baker, 1986). McCracken (1987) noted no significant genetic heterogeneity among either male or female greater white-lined bats in Trinidad. However, the among-colony allelic composition of male groups has greater variance than that of female groups, indicating that males within a group are more closely related (McCracken, 1987). Relationships among members of the family Emballonuridae, including *S. bilineata,* were assessed by use of protein electrophoresis and immunology, and three major subdivisions within the family were identified. The eight genera from the New World, including *S. bilineata,* comprise one monophyletic group, the Old World genera *Taphozous* and *Saccolaimus* make up the second group, and the Old World genera *Emballonura* and *Coleura* form the third group. The Old World subdivision composed of *Emballonura* and *Coleura* is more closely related to the New World subdivision than to the other Old World group (Robbins and Sarich, 1988).

REMARKS. The name *Saccopteryx* refers to the glandular sac in the antebrachial membrane. The specific epithet *bilineata* refers to the two distinct longitudinal stripes on the dorsum (Jaeger, 1955). Another common name for this species is the white-lined sac-winged bat.

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