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Carollia perspicillata.

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Carollia Gray, 1838

Carollia Gray, 1838:488. Type species *Carollia braziliensis* Gray (=*Vespertilio perspicillatus*).
Hemiderma Gervais, 1855:43. Type species *Hemiderma brevicaudum* Wied, 1821 (=*H. perspicillatum*).

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Phyllostomidae, Subfamily Carolliinae (2 genera). The genus *Carollia* contains four recognized species *C. perspicillata, C. brevicauda, C. subrufa,* and *C. castanea* (Pine, 1972). A key to the species follows (Hall, 1981; Pine, 1972):

1. When viewed from above, i2 obscured by cingulum of canine, or upper toothrow straight; lower jaw generally V-shaped .... *C. perspicillata*
   When viewed from above, i2 easily visible; upper toothrow bowed lingually or with a distinct notch or step in labial outline; lower jaw tending to be U-shaped 2
2. Labial outline of upper toothrow with distinct notch or step; p2 twice height of m1; occlusal surface of m1 with straight profile .... *C. castanea*
   Labial outline of upper toothrow curved, without notch or step; p2 less than twice height of m1; occlusal surface of m1 with cusp or cusps, resulting in jagged profile 3
3. Pelage long, thick, and fine; forearm hairy; hair on nape of neck with broad dark basal band contrasting strongly with and sharply demarcated from broad whitish band distal to it .... *C. brevicauda*
   Pelage short, sparse, and coarse; forearm naked or sparsely furred; hair on nape of neck with narrow, generally indistinct basal band, not strongly demarcated from paler band distal to it .... *C. subrufa*

Carollia perspicillata (Linnaeus, 1758)

Short-tailed fruit bat

Vespertilio perspicillatus Linnaeus, 1758:31 (based on *Vespertilio americanus vulgaris* Seba, 1734:90, South America). Type locality "America" restricted to Surinam (Thomas, 1911). *Hemiderma brevicaudatum* (Thomas, 1892:315) is now regarded as the Linnean type for *C. perspicillata.*
Carollia azteca Saussure, 1860:480. Type locality "probably Perez, Vera Cruz, Mexico."
Hemiderma tricolor Miller, 1902:408. Type locality "Sapucay, Paraguay."

CONTEXT AND CONTENT. Context in generic summary. Pine (1972) noted that putative subspecies (*C. p. azteca, C. p. perspicillata,* and *C. p. tricolor*) intergrade. In a reanalysis of the specimens, McLellan (1984) concluded that no subspecies exist on a basis of cranial characteristics.

DIAGNOSIS. The key is useful when skins and cleaned skulls of individuals from the same region are available (McLellan, 1984), but Koopman (1978) noted that the skull characters used by Pine (1972) did not clearly distinguish between *C. brevicauda* and *C. perspicillata* from Peru. Barbee and Fugler (1977), analyzing nine meristic characters in 17 populations of *C. perspicillata, C. castanea,* and *C. brevicauda* from Central and South America, also noted that *C. perspicillata* is poorly differentiated from *C. brevicauda.* Character convergence or hybridization is possible between these two species (McLellan, 1984; Pine, 1972). Basilar length (181.1 ± 0.86 mm ± 2 *SE*), length of maxillary toothrow (75.3 ± 0.42), length of ventral rostral (63.0 ± 0.38), mandibular length (144.1 ± 0.76), coronoid angular distance (57.0 ± 0.51), and coronoid height (51.5 ± 0.50) of cranium best separate *C. perspicillata* from congenerics (McLellan, 1984).

Field identification can be difficult. Among 6,684 specimens from Venezuela, 1,797 were not identifiable to species (Handley, 1976). *C. perspicillata* can generally be identified from congenerics by: length of forearm, 43–46 mm; a basal dark band on interscapular hairs is narrow and not strongly demarcated from the succeeding band; sparse hairs are present on the forearm; hairs on the back are short; crowns on the middle pair of lower incisors are about twice as wide as those on the outer pair; the greatest length of skull (including upper incisors) is >24 mm (Owen et al., 1984). On average, *C. perspicillata* is 19% heavier and has forearm 9.2% longer than *C. subrufa.* The best criteria for separating the two species in the field may be: the lower inner incisors of *C. perspicillata* are larger than the outer incisors and are crowded and unequal in size while those of *C. subrufa* are spaced and equal in size (Pine, 1972; Fleming, 1988).

GENERAL CHARACTERS. *Carollia perspicillata* is a robust bat, small to medium in size (mass about 18.5 g; total length, 66–95 mm; Fig. 1). The ears are relatively short (17–22 mm), wide, and pointed. The noseleaf is fairly short and triangular. The lower lip is V-shaped and has a large central wart bordered by a row of small and rounded warts on a naked pad. The fur is dense, soft, and 8 mm long in middorsal area. Coloration ranges from almost black, through browns, to rusty or gray (Hall, 1981). Bright or pale orange individuals are common in some areas (Fleming, 1988). A partially albino specimen was identified (Goodwin and Greenhall, 1961). Tri-colored dorsal hairs are dark at the base, paler in the

FIG. 1. Adult *Carollia perspicillata* feeding on *Piper tuberculatum.* Photograph by Merlin Tuttle.

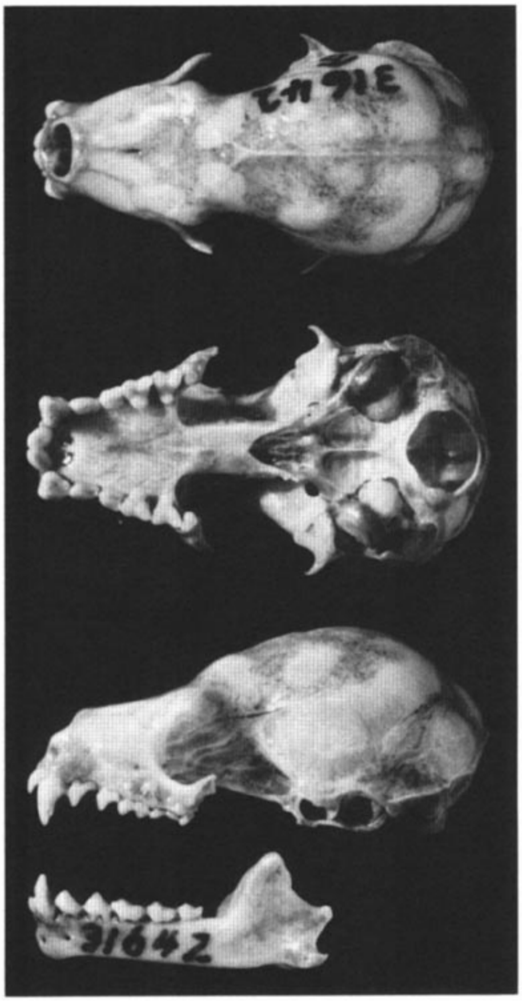

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of lower jaw of *Carollia perspicillata* (Male, Royal Ontario Museum 31642, Nappi Creek, Kanaku Mountains, Guyana). Greatest skull length is 12.8 mm. Photographs courtesy of Royal Ontario Museum.

middle, with the terminal band darkest. The upper parts are often buff and ventral hairs lack banding. Facial stripes are absent. The tail is one-half (11–14 mm) the length of the naked interfemoral membrane (Barquez, 1977; Goodwin and Greenhall, 1961; Hall, 1981; Miller, 1907). Mass is 18.9 g (n = 1,364) for males and 18.5 g (n = 691) for females. Forearms are furred dorsally and average 42.0 mm (n = 1,660) for males and 42.3 mm (n = 1,639) for females (Fleming, 1988). The longest finger is 95–101 mm. The length of tibia is 14.1–19.9 mm and it has rather large feet (12–17 mm). The calcar is about 8 mm in length. The skull is relatively robust and the length of rostrum is nearly 66% of the braincase (Fig. 2). The braincase rises above the frontal region; the zygomata are incomplete. Male and female cranial measurements (in mm) from 15 localities are: greatest length of skull, 21.4–25.2; condyloincisive length, 19.3–22.7; length of palate, 9.5–11.7; breadth of mastoid, 10.2–12.4; width of braincase, 9.0–10.4; postorbital constriction, 5.0–6.1; depth of the braincase, 9.3–10.8; length of mandible, 13.8–16.2; depth of mandibular, 1.8–3.3; length of mandibular toothrow, 8.1–9.7 (Pine, 1972). Dry specimens are 1.5% less in length of forearm than fresh ones (Arata, 1968).

The permanent dental formula is i 2/2, c 1/1, pm 2/2, m 3/3, total 32. The jaws are short with robust and highly specialized cheek teeth. U1 has a recurved point. Upper teeth are crowded and the toothrow is relatively straight. Upper incisors fill the space between the canines, while lower incisors are small, notched, and form a convex row between the canines. Upper and lower molars do not conserve the primitive W-shaped ectolyph. The outer edge of the first two molars is raised above the inner edge (Fleming, 1988; Goodwin and Greenhall, 1961).

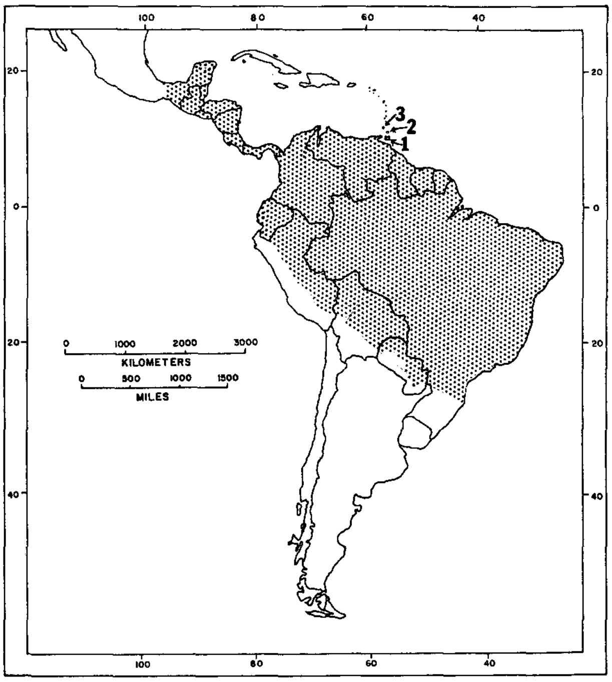

FIG. 3. Geographic distribution of *Carollia perspicillata* in Central and South America. Distribution in Anitllian Islands includes Trinidad (1), Tobago (2), and Grenada (3); modified from McLellan, 1984).

Sexual dimorphism is geographically variable. In West Indies, females are larger than males in length of forearm, upper toothrow, and cranial measurements (Allen, 1911; Swanepoel and Genoways, 1979; Taddei, 1975). In Columbia, there are no sex differences in size and color (Tamsitt and Valdivieso, 1963). In most areas, males are heavier than females, the lengths of forearms are equal, but wings of females are longer relative to body size (Pine, 1972). Rostral breadth is most dimorphic, but sexual dimorphism accounts for only 6.8% of observed variation between males and females (McLellan, 1984). Individuals are larger in the northern part of their range, complicating inter-sex comparisons (Owen et al., 1984; Pine, 1972).

DISTRIBUTION. *Carollia perspicillata* has a primarily continental distribution from Veracruz and Oxaca, Mexico, to southern Bolivia, Paraguay, and Brazil where it is one of the most commonly captured bats. It is present in Trinidad, Tobago, and Grenada (Fig. 3). One specimen was reported from Jamaica (Allen, 1911, 1939; Dobson, 1878) and three individuals from the island of Redonda (Hahn, 1907), but its presence there is doubtful (Jones and Phillips, 1970; Koopman, 1968; Pine, 1972). There is no fossil record for the species.

FORM AND FUNCTION. The brain is characterized by short cerebral hemispheres, a simple cerebellum with primary lobes only, and an interhemispheric sulcus including shallow cingulate and callosal sulci and a thin cortical cell layer (McDaniel, 1976). This bat has a high brain/body ratio compared to insectivores (Eisenberg and Wilson, 1978). The large visual and olfactory brain centers may have evolved in response to requirements for orientation, food location, and social interactions (Baron and Jolicoeur, 1980; Pirlot and Pottier, 1977).

Carollia perspicillata has an excellent sense of smell. It can detect a threshold concentration of 4 × 10^{11} molecules of isopentylacetate/cm^3 air (Laska and Schmidt, 1986). Decreasing relative humidity reduces performance in orientation tests using olfactory cues (Laska et al., 1986). The olfactory organ is similar to other phyllostomids with three endoturbinals, two ectoturbinals, a well developed vomeronasal organ, and nasopalatine ducts (Kämper and Schmidt, 1977). The vomeronasal organ complex is 1.76-mm long and includes an accessory olfactory bulb. Anteriorly, the tubelike vomeronasal cartilage encloses the organ (Bhatnagar, 1980). The morphology of the vomeronasal neuroepithelium is similar to other mammals, but differences in the configuration of apical poles of cells exist. The form of receptor cell microvilli and the ethmoid bone indicate high olfactory sensitivity (Bhatnagar et al., 1982; Bhatnagar and Kallen, 1974).

Visual acuity, brightness discrimination, and pattern vision are good (Chase and Suthers, 1969; Suthers and Chase, 1966; Suthers and Wallis, 1970; Suthers et al., 1969). Optomotor responses show the minimum separable angle to be 0.7° (Suthers, 1966). The light-tolerant retina is progressively more responsive to wavelengths between 540 and 620 nm (Hope and Bhatnagar, 1979*a*, 1979*b*). The retinal projections to the pars ventralis and dorsalis of the lateral geniculate nucleus are crossed. The superior colliculus is larger and more differentiated than that of *Myotis sodalis*, having few degenerating fibers present on the ipsilateral side and some degenerating axons to the contralateral superior colliculus (Kirtland and Campbell, 1969). There are three Meibomian glands per eye, two small anterior and one large posterior (Desch and Nutting, 1972).

The volume of the auditory structures indicate a less specialized auditory apparatus than in insectivorous bats (Baron, 1974). There is no correlation between echolocation and cochlear dimensions (Pye, 1967). Echolocation pulses are short, frequency-modulated, and contain several harmonics of low intensity (3.6 dynes/cm^2; Griffin and Novick, 1955). These bats are classed as whispering (Griffin, 1958) and the echolocation as clutter rejecting (Simmons and Stein, 1980). Cruising pulses are 0.5–1.0 ms long and first, second, and third harmonics sweep from 48 to 24 kHz, 80 to 48 kHz, and 112 to 80 kHz, respectively. Most energy is in the second and the third harmonics (Pye, 1967). Echolocation calls are emitted through the mouth or nostrils; removal of the nose leaf has no marked effect (Griffin and Novick, 1955). *C. perspicillata* has its best hearing in the 80 kHz range. Response recovery is rapid (2–3 ms). The colliculus is relatively insensitive to angular changes of the signal, while the auditory nerve response is sharply sensitive (Grinnell, 1970). It can detect wires as small as 0.175 mm at 1 m (Griffin and Novick, 1955).

A specialized primary dentition, particularly the upper and lower canines and upper outer incisors, allows babies to cling to the mother. The deciduous formula is di 2/2, dc 1/1, and dpm 3/2, total 22. Shedding begins with the lower deciduous premolars during the first 2 weeks, progressing to the lower canines, upper premolars, and upper inner incisors. Permanent dentition emerges first on the maxilla and is complete by 31 days (Kleiman and Davis, 1979). The complex enamel ultrastructure display mostly completed, rounded prisms, some with a prism-in-a-prism configuration (Lester et al., 1988).

The tongue is broad with a rounded apex and a shallow longitudinal depression on the upper surface. Horny, filiform, small bifid flattened, scale-like, vallate, and fungiform papillae are found. Based on tongue structure, *C. perspicillata* lies intermediate between insectivores and nectarivores (Park and Hall, 1951). Histology of salivary glands is lacking.

The stomach is large, triangular, covered with numerous folds, and has an enlarged cardiac vestibule. The pyloric portion is elongate and recurved anteriorly and the pyloric sphincter has a uniform circumference through its length (Forman et al., 1979). The pyloric and cardiac orifices are in the same plane (Park and Hall, 1951). Mature chief, parietal (mature and immature), mucous neck, and mucous epithelial cells compose the gastric mucosa (Phillips et al., 1984). Mucous cells are significantly smaller in size and number compared to other species and a sulfonated component is lacking in mucous neck cells. An unusual entero-endocrine cell type is present. Brunner's glands are sparse and Peyer's patches are large and widely distributed (Forman, 1974*a*, 1974*b*). There is no caecum, but a small ampulla lies at the junction of the small and large intestines (Forman et al., 1979). Intestinal length is 20.0 cm and the average pH is 6.2 (Klite, 1965). The mean intestinal transit time is 20.6 min (Fleming, 1988).

The wings are generalized for handing food and climbing, as well as for flying (Vaughan and Bateman, 1970). The wing area is 159 cm^2, wing span is 30 cm, tip index is high (2.00), and aspect ratio (1.99) and wing loading (0.09 g/cm^2) are low (Barquez, 1977; Findley et al., 1972; Smith and Starrett, 1979). In the process of hanging up, both wings beat with equal strength (Gould, 1960). The skeletal system reflects flight adaptations (Walton and Walton, 1968, 1970). The mean foot pad swelling is 0.048 ml (McMurray and Thomas, 1976).

The short-tailed fruit bat drinks less than insectivorous bats due to its high dietary water content. Average natural urine concentration is 14.5 mEq Na/l and 58.7 mEq K/l. The mean urine osmotic pressure is 238 mOsm/kg. The highest urine concentration is reached after 21–29 h without food or water (Studier and Wilson, 1983). Basal metabolism is 2.89 ml O_2 g^{-1} h^{-1} and at ambient temperatures of 19–26°C and relative humidity of 92–98%, and conductance is 0.35 ml O_2 g^{-1} h^{-1} °C^{-1} at a body temperature of 36.4°C (McNab, 1969). *C. perspicillata* is an effective thermoregulator in the range from −2 to 30°C (Arata and Jones, 1967; Herbst, 1983; McNab, 1969), but it shows intermediate responses to decreasing ambient temperatures (Studier and Wilson, 1970). This bat uses torpor when food is lacking or limited (Rasweiler, 1973). Body mass varies seasonally; males and nonpregnant females are 7–17% lighter during dry season and old adult males are heavier than young adults during the wet season. Daily energy budgets (DEB) are about 42 and 47 kJ for March and June; maintenance and flight are the most costly activities. DEB's of lactating females are two times larger than other bats, but on an annual basis their energy budgets are 26% higher (Fleming, 1988).

Electrophoresis of hemoglobin produces an anodal band corresponding to the human S band; hemoglobin patterns reflect taxonomic relationships (Tamsitt and Valdivieso, 1969). McMurray and Thomas (1979) studied delayed hypersensitivity to bovine serum albumin and purified protein derivative antigens. Noninvasive electrocardiograms were performed on anesthetized individuals and a mean heart rate of 419.71 beats/min was measured (Cook et al., 1987).

REPRODUCTION AND ONTOGENY. Long term studies in northern Costa Rica and Panama show two reproductive periods with the greatest proportion of pregnant females in June–August coinciding with peak fruit production. A second breeding period occurs during the mid or late dry season (February–May) when flowers are abundant (Fleming et al., 1972; Heithaus et al., 1975; Williams, 1986; Wilson, 1973). The same pattern was found in Brazil (Willig, 1985), but no clear reproductive period was noted in Trinidad, Panama, and Sao Paolo (Asdell, 1946; Bloedel, 1955; Taddei, 1976). Three birth peaks were noted in a captive colony (Kleiman and Davis, 1979).

Ovulation normally alternates between the two ovaries with the release of a single ovum (Bleier, 1979), but the occurrence of one developed corpus luteum on each ovary suggests that twinning can occur (de Bonilla and Rasweiler, 1974). Allen (1939) reported two embryos each in five females from the Amazon Valley. Estrus appears to be postpartum (Rasweiler and de Bonilla, 1972), It is unknown whether ovulation is spontaneous or induced. Fertilization is probably immediate, but cleavage is slow. The blastocyst is apparent and the zona pellucida is lost 10 days postcoitum. Implantation occurs between the end of the oviduct and the main uterine cavity (Bleier, 1979; de Bonilla and Rasweiler, 1974). The placenta is likely discoidal and endotheliochorial (Bleier, 1979; Wimsatt, 1958). During the 115–120 day gestation, females gain about 30% of their initial mass and weigh 14.5–23.1 g. The fetus lies transversely and is palpable 5–6 weeks before parturition (Kleiman and Davis, 1979). Mother's nipples are pink and fur-free 2 days before birth. At parturition, the mothers eat the placenta and lick the newborn. The umbilical cord dries and falls within 24 h. Females produce a thick milk for 21–49 days and a thin milk for the remaining 42–72 days. Milk is high in fat and carbohydrates, but low in protein content (Glass and Jenness, 1971; Jenness and Sloan, 1970; Jenness and Studier, 1976). The dark pigmentation and fur reappears on the mammae 36–66 days after parturition and they return to the prepartum condition after 64–87 days.

Newborns are precocial with eyes and ears open. They have dense fur on their backs and sparse fur on their venters and muzzles (Kleiman and Davis, 1979). The dark brown juvenile pelage appears after 7–10 days, but a second generation of hair has not been observed (Klima and Gaisler, 1968). Newborns weigh about 5.0 g or 28% of the mother's postpartum mass. Growth is rapid; the adult mass is attained after 10–13 weeks. The newborn forearm is 22.4–27.5 mm or 60% of adult length. The forearm grows 0.8 mm/day; body mass increase is 0.3 g/day. At 6 weeks, forearm growth is essentially completed. The young begin to fly when the forearm length and mass are 93.4% and 63.0%, respectively, of adult size (Kleiman and Davis, 1979). The infant hangs on the nipples during the first days and is groomed (Porter, 1979*a*; Kleiman and Davis, 1979). The typical carrying position (at rest or in flight) is crosswise on the ventral thorax. Females do not place their young in crèches but commonly fly with them. They may transfer their baby from day to night roosts while foraging (Kleiman and Davis, 1979), but mothers usually leave their young in the roost while feeding (Porter, 1979*a*). The young will cling to the mother for 23 days, during which time it attains 57% of the mother's mass, but after 7–18 days they begin to hang alone (Kleiman and Davis, 1979; Porter, 1979*a*). Females were seen nursing babies that were not their own on two occasions, but this is uncommon (Williams, 1986). Young make short, unsteady flights away from the roost after 2.5–4 weeks; mothers sometimes accompany the infants (Porter, 1979*a*). Volant young were captured at 23–31 days of age. They are weaned at about 2 months and infant mortality is highest at this period (Kleiman and Davis, 1979). Postweaning mortality is the most likely cause of a shift from a male bias at birth (65.6%) to a 1:1 sex ratio among adults (Fleming, 1988). Young stay within the parental harem for up to 16 weeks before dispersing to other groups or roosts; females are more inclined to disperse to new roosts than males (42% vs 11%; Fleming, 1988). Some females become pregnant at 8–9 months (Porter, 1979*a*). All females reach sexual maturity by 1 year; it is suggested that they attain sexual before physical maturity. Males become mature between 1 and 2 years when bone growth is complete (Taddei, 1976). The spermatozoa structure is: head narrow, neck short, midpiece of moderate length with distinctive tail junction (Forman and Genoways, 1979). Adult male testes are largest just before females enter estrus. Old adults have a closer synchronization between ovulation in females and peak spermatogenesis than do young (Fleming, 1988; Williams, 1986). Parturition may occur at 11–16 months. The inter-birth interval ranges from 115–417 days (Kleiman and Davis, 1979; Porter, 1979*a*).

ECOLOGY. *Carollia perspicillata* is found in moist evergreen and dry deciduous forests from Mexico to southern Brazil, but is typically most common in second growth (DosReis and Guillaumet, 1983; Fleming, 1988; LaVal and Fitch, 1977; Pine, 1972). Its presence seems associated with stagnant waters and free internal space (Marques, 1985). It is most abundant below 1,000 m, but ranges to 1,550 m in Peru and 2,150 m elsewhere (Koopman, 1978; McLellan, 1984; Pine, 1972). This bat is one of the most common caught at ground level, where it forages on a large variety of fruits, some flowers, and some insects. It is a generalist and feeds on at least 23 species of fruits in Trinidad (Goodwin and Greenhall, 1961; Greenhall, 1956, 1957), 22–24 species in Panama (Bonaccorso, 1979; Fleming et al., 1972), 15–18 species in Costa Rica (Fleming, 1988) and 28 species in Brazil (DosReis and Guillaumet, 1983). In Costa Rica and Panama, over 50% of dietary fruits are produced on low trees and shrubs, classing this bat in the ground story frugivore guild (Bonaccorso, 1979). This species preferentially feeds on fruits having high protein and low fiber content and an extended fruiting season (Bonaccorso and Gush, 1987; Fleming, 1988). The genera *Piper* and *Solanum* form the mainstay of the diet through much of its range, followed by a large number of small-seeded secondary species (e.g., *Cecropia*). Fleming (1988) lists 50 fruits of 24 families used by this bat. Fruit presentation experiments show that this bat searches preferentially for low-density species ripening few fruits nightly (such as *Piper*; Fleming et al., 1977). Bats consume about 35 fruits nightly and may disperse 350—2,500 seeds depending the species (Fleming, 1988). *C. perspicillata* is the major disperser for *Piper amalago* seeds (Fleming, 1981). It does not disperse *Dypteryx panamensis* (Bonaccorso et al., 1980) and damages *Anacardium excelsum* seeds (Humphrey and Bonaccorso, 1979). Gut passage increases germination success (32% versus 28%) and decreases germination time (13 versus 36 days) for *Piper aduncum* (DosReis and Guillaumet, 1983), but Fleming (1988) did not confirm this for other species.

Carollia perspicillata supplements its diet with nectar and pollen during the dry season when fruit availability is low and flower production peaks (Fleming and Heithaus, 1986; Heithaus et al., 1975; Sazima, 1976; Sazima and Sazima, 1978). Due to its abundance, this species may be an important pollinator of *Ochroma lagopus, Hymenaea courbaril, Bombacopsis quinatum, Ceiba pentandra, Pseudobombax septinatum, Crescentia* sp., and *Manilkara zapota* in Costa Rica (Heithaus et al., 1975). Fleming (1988) lists 11 flower species in six families that are visited by this bat in Costa Rica. Insects are frequently included in its diet (Arata et al., 1967; Ruschi, 1953). Insects constitute 10% of stomach contents in the wet season and 40% in the dry season in Costa Rica (Fleming et al., 1972), but this may be underestimated because bats ingest only the soft parts of hard-bodied insects (Ayala and d'Allessandro, 1973). Insects may supplement the low-protein content of a fruit diet (Thomas, 1984), but Herbst (1985) estimates that non-lactating individuals can obtain sufficient protein from most fruits and that *Piper* can supply the requirements for lactating females.

The short-tailed fruit bat has a relatively large diet overlap with *C. subrufa, Glossophaga soricina,* and *Sturnira lilium.* Other potential food competitors include at least seven species of mammals and six species of birds (Fleming, 1988). *C. perspicillata* has been observed roosting with at least 35 other species in eight families. Predator-free roost space may be a limiting resource and can lead to competition between *C. perspicillata* and other bats. *Phyllostomus hastatus* and *Desmodus rotundus* have been reported displacing *C. perspicillata* from hollow tree roosts (Humphrey and Bonaccorso, 1979). *G. soricina* may compete for the same roosting sites. Known or potential predators include snakes (*Constrictor constrictor, Trimorphodon biscutatus*) birds of prey (*Tyto alba, Ciccaba virgata, Pulsatrix perspicillata, Micrastur semitorquatus*), nocturnal arboreal mammals (*Didelphis virginiana, Caluromys derbianus, Potos flavus, Philander opposum*) and the false vampire bat (*Vampyrum spectrum*; Fleming, 1988). A captive *C. perspicillata* was killed by a *P. hastatus* (Allen, 1939) and another captive specimen was bitten on the back by *D. rotundus* (Goodwin and Greenhall, 1961). The impact of predators on populations or behavior is unknown.

Carollia perspicillata is characterized by a low fecundity and long life span. The annual mortality rate is 53% for the first 2 years of life, and 22% for the following years. Life expectancy is 2.6 years at birth and the maximum life expectancy is near 10 years. Survivorship of males and females is similar (Fleming, 1988).

A large diversity of ectoparasites reflects *C. perspicillata*'s great ecological flexibility (Wenzel et al., 1966). The ectoparasite fauna includes 27 species of mites, 7 ticks, and 24 bat flies (Brennan, 1970; Desch et al., 1971; Dusbabek and Lukoschus, 1975; Lukoschus et al., 1980; Webb and Loomis, 1977). The most common streblid flies were: *Trichobius joblingi* (74.44%), *Speiseria ambigua* (10.78%), and *Strebla carollia* (8.15%; Wenzel et al., 1966). Three streblid flies (*T. joblingi, S. ambigua,* and *S. guajiro*) are specific to *C. perspicillata*; females are significantly more parasitized than males (3.5 versus 2.1 flies; Fritz, 1983). High ectoparasite loads could cause females to switch roosts (Fleming, 1988).

Endoparasites include nematodes, protozoans, and digenic trematodes (Ubelaker et al., 1977). Specimens from Columbia were infected with trypanosomes (1.8%), suggesting that *C. perspicillata* is a reservoir for these parasites (Marinkelle, 1982) but this was not confirmed by Avila et al. (1986). The average number of all intestinal bacteria is about 1,000. Seven bacteria were found (*Escherichia, Klebsiella-Aerobacter-Seratia, Proteus, Pseudomonas, Alcaligenes, Bacillus, Clostridium, Enterococcus*). The fungus, *Histoplasma capsulatum,* was present in one individual at a concentration of 1,000 spores/intestinal content (Klite, 1965). Only 7 of 141 bats had this fungus in the lungs, liver, and spleen (Klite and Diercks, 1965). A low infection rate (1.2% of 625 bats) was also confirmed by Hasenclever et al. (1967, 1969). Colonial individuals are more susceptible to infection (Tesch et al., 1968). Other fungi found on *C. perspicillata* are *Scopulariopsis* from Mexico and *Cryptococcus* and *Candida* from Colombia (Jones, 1976). Antibody tests indicate that this bat is rarely infected with Venezuelan encephalitis virus (Scherer et al., 1971); however, a new strain of Venezuelan equine encephalitis was isolated from *C. perspicillata* from Brazil and *Jurona* virus was reported from Brazil (Calisher et al., 1982). The short-tailed fruit bat is known to harbor rabies virus in Trinidad and Colombia (Downs et al., 1963; Goodwin and Greenhall, 1961; Greenhall, 1957).

Carollia perspicillata keeps well and breeds in captivity on a reversed 12L:12D cycle, a temperature of 23–28°C, and a relative humidity between 60 and 90%. Chopped fruits supplemented with protein, minerals, and vitamins provide an adequate diet (Greenhall, 1976; Porter, 1978; Rasweiler and de Bonilla, 1972).

BEHAVIOR. *Carollia perspicillata* is a gregarious bat with generalized day roost requirements. Groups of 10 to over 100 bats commonly roost in caves, hollow trees, tunnels, road culverts, and, less commonly, among rocks, under leaves, and in buildings. The diurnal activity budget is dominated (98% of time) by nonaggressive activities such as resting, alert scanning, and grooming, but includes crawling, scent marking, investigation of females, and vocalizing (Porter, 1979*a*). Significant daily, seasonal, and sexual variation exist. Territorial males are the most active individuals (Fleming, 1988).

Studies in captivity (Porter, 1978, 1979*a*, 1979*b*) and in the wild (Williams, 1986) indicate that this species has a polygynous (harem) social organization. Males defend protected roosting sites where females aggregate, suggesting a resource defence system. Two types of roost sites exist. Harem sites are used by a single territorial adult male, one or several females, and juvenile offspring. Bachelor sites are used by adult and subadult males that do not have harems. Young females may join these latter groups seasonally. Only 12–17% of adult males have harems (Fleming, 1988). These groups are typically located in the least disturbed areas highest above the floor and far from the roost entrance (Porter, 1979*a*; Williams, 1986). An average of 2.16 females/harem is found in the wild, but some contain 18 (Fleming, 1988). In captive colonies, harems vary from 1 to 5 females (Porter, 1979*a*, 1979*b*). Males actively recruit females by hovering and vocalizing, suggesting that females may choose harems on the basis of male quality (Porter, 1979*a*), but Fleming (1988) and Williams (1986) postulated that choice depends on roosting site quality. Females change harems on average every 17 days (Porter, 1979*a*) and can occupy 10 different harem sites in a season (Williams, 1986).

Territorial males are faithful to a given roost for up to 277 days and harem males defend their territory even in the absence of females (Williams, 1986). They actively defend their harem from intruders by nosing, wing shaking, boxing, and vocalizing (Porter, 1978, 1979*a*; Williams, 1986). The rate of fighting following a harem takeover drops from 25.9 bouts/h to 3.5 bouts/h over 2–4 weeks (Williams, 1986). Adult females tend to move from caves during the wet season to hollow trees during the dry season (Fleming, 1988). In captivity, they rarely leave the harem between birth and weaning (Porter, 1979*a*). Bachelor males are much less faithful to a roost than harem males. Harem males possibly guard offspring they did not father (Porter, 1979*a*). Studies determining paternity indicated that 25% of the offspring in harems were not fathered by the harem male (Porter and McCracken, 1983). Courtship and copulation occurred up to five times/h. During the lactation period, harem males guard the young while females forage (Porter, 1979*a*).

Mother-young communication is mediated through sounds, but olfactory cues may also be important. The vocal repertoire includes FM pulses, whines, warbles, trills, screeches (or "buzz"), and double-note calls in the 12–40 kHz range. Newborn vocalizations are similar to those of adults after only a few days (Gould, 1975; Gould et al., 1973; Porter, 1979*b*). Distinct isolation calls from newborns have not been described (Gould, 1975; Porter 1979*b*). Both mothers and harem males respond to their own young who are calling, suggesting individual vocal signatures. Males were observed vocalizing, wing-poking, and shoving to reunite mothers and their young (Porter, 1979*b*). Interactions among adult females are poorly known; aggression is low within harems but higher between harems (Porter, 1979*a*; Williams, 1986; Fleming, 1988).

Carollia perspicillata leaves the day roost to forage soon after sunset, creating an early evening activity peak. No other clear peaks follow (DosReis and Guillaumet, 1983; Heithaus and Fleming, 1978). Females and bachelor males commute to a feeding area with exploratory flights constituting only 1.5% of 393 km flown by tagged bats (Heithaus and Fleming, 1978). They then search, harvest, and carry a fruit to a feeding roost and repeat these feeding passes 40–50 times in a night (Charles-Dominique, 1991). They return to the day roost between 0300 h and 0500 h after ingesting at least their own mass in fruit pulp and seeds. *C. perspicillata* may carry fruits to its day roost at the end of the night (Greenhall, 1956). Most individuals forage within 2 km of the day roost (Fleming and Heithaus, 1986). Mean recapture distances vary from 167 to 310 m and are correlated with body size (Fleming et al., 1972; Heithaus et al., 1975; LaVal, 1970; LaVal and Fitch, 1977). During the dry season in Costa Rica, foraging bats travel about two times farther than during the wet period, but in French Guiana there were no seasonal differences in the number of feeding flights nor in the time spent flying (Charles-Dominique, 1991). The use of feeding roosts is probably the result of a compromise between predator pressure, traveling distances, and seed dispersal (Fleming, 1982). Feeding roosts are used for brief periods in a night. *C. perspicillata* is an intermittent rather than continuous feeder (Bonaccorso and Gush, 1987; DosReis and Guillaumet, 1983). At Santa Rosa, Costa Rica, feeding roosts were in low vegetation tangle or in canopies of tall trees (Janzen et al., 1976), typically 20–50 m from a fruiting tree (Heithaus and Fleming, 1978). The harem male returns to the harem site between feeding bouts and is a central place forager. Bats forage every night, independent of weather and moonlight conditions, but on nights with a full moon, foraging distances are reduced by 80% (Heithaus and Fleming, 1978).

Feeding rates are 14–15 min/fruit (range, 8.9–37.2). Large fruits can be eaten in the parent tree and often <50% is consumed (Fleming, 1988; Goodwin and Greenhall, 1961). Small fruits are carried to the feeding roost and bats are often captured with *Piper*, *Vismia*, or *Solanum* fruits in their mouths (DosReis and Guillaumet, 1983). Greenhall (1957) listed food preferences and identified which parts of fruits are eaten. Ripe fruits are found by olfaction (Wolff, 1981). The short-tailed fruit bat is capable of forming a conditioned taste aversion when a specific food is associated with illness (Terk and Green, 1980).

GENETICS. The fundamental number is 36 with the female and male 2n condition being 20 and 21, respectively. Females are XX and males XY_1Y_2. Nine autosomal pairs are formed by four metacentric, two submetacentric, and three subacrocentric pairs. The X chromosome is subacrocentric with a secondary constriction on the long arm; Y_1 is medium acrocentric and Y_2 is small acrocentric (Baker, 1967; Baker and Hsu, 1970; Hsu et al., 1968; Yonenaga et al., 1969). The chromosomes are recognizable and their relative sizes (% haploid female set) are: chromosome 1 = 26.5; 2 = 14.6; 3 = 13.5; 4 = 8.0; 5 = 6.5; 6 = 4.8; 7 = 4.0; 8 = 3.5; 9 = 2.8; X = 15.7; Y_1 = 7.1; Y_2 = 1.5; $Y_1 + Y_2/X = 0.55$ (Yonenaga et al., 1969). The additional Y is the homolog of an autosome translocated to the X element (Hsu et al., 1968). Nucleolus organizer regions are present on the X chromosome (Goodpasture and Bloom, 1975; Hsu et al., 1975). The order of the termination sequences of DNA replication is: euchromatin > G-bands > C-bands > facultative heterochromatin (Pathak et al., 1973; Stock, 1975). Using a female for C-banding procedures, it was shown that the euchromatic segments lost a significant amount of DNA. Centromeric and interstitial C-bands are present on chromosome 1 and terminal C-bands on chromosomes 2 and 3. Several large chromosomes are the sites of discrete block G-bands (Pathak and Arrighi, 1973). *Carollia*, *Choeronycteris*, and *Choeroniscus* have similar karyotypes (Baker, 1967, 1979; Baker and Bleier, 1971). Albumin, alpha glycerphosphate dehydrogenase, and phosphoglucomutase-1 are all highly polymorphic (Honeycutt and Sarich, 1987; Straney et al., 1979; Valdivieso and Tamsitt, 1974).

REMARKS. *Vespertilio perspicillatum* (=*V. perspicillatus*) represented two to three species belonging to two to three different genera (Pine, 1972). One of these species had facial stripes, giving rise to the misleading specific name *perspicillatum* which indicates the presence of white stripes on the face (Saint-Hilaire, 1810). Other common names used in the past are: Seba's short-tailed bat, Linnaeus short-tailed fruit bat, Aztec short-tailed bat, short-tailed leaf-nosed bat, and little short-tailed bat.

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