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APPENDIX 1

Specimens examined.

Acacia collinsii × *Acacia hindsii*—Mexico: Guerrero: Lok. 7, Mirador, 5 km S de la Base Naval de Icosos, 17 September 1984, *L. Brimer s. n.* (ILL).

Acacia collinsii × *Acacia pennatula*—Mexico: Chiapas: El Chorreadero: 5.6 miles E of Chiapa de Corzo along Mexico Hwy. 190, altitude 2,500 feet, 10 April 1965, *D. E. Breedlove 9638* (F, US); Unos 5 km al N de Tuxtla Gutiérrez, altitude 650 m, 11 February 1951, *F. Miranda 6889* (US). Oaxaca: 50 miles E of Tehuantepec on Hwy. 190, 3 August 1975, *Seigler et Holstein 9782* (ILL).

Acacia cornigera (?) × *Acacia pennatula*—Mexico: Veracruz: 24.3 miles from Veracruz on Hwy. 140, 16 September 1984, *Seigler, Berlocher et Nickrent 12224* (ILL).

Acacia × *gladiata* (*Acacia cochliacantha* × *Acacia hindsii*)—Mexico: Oaxaca: 3 miles N of Puerto Escondido, 29 May 1980, *Seigler, Richardson et Thompson 11566* (ILL). Sinaloa: 1922, *J. G. Ortega 4884* (US); specimens grown in greenhouse from seeds collected from a plant growing in western Mexico a bit south

of Mazatlán, 19 April 1968, *D. H. Janzen 151* thru 168 (EIU).

Acacia × *standleyi* (*Acacia hindsii* × *Acacia pennatula*)—Guatemala: Dept. Guatemala, 1939, *I. Aguilar 212* (F); Dept. Escuintla, in pasture above Palin, altitude 1,500 m, 16 December 1938, *P. C. Standley 60100* (F). Honduras: Dept. Comayagua, tree in dry gulch near San Luis, close to the river, 13 April 1974, *D. Hazlett 1445* (MO). Mexico: Chiapas: a unos 3 km de Ocosingo, por la orilla de la carretera que va a Tonina, 23 May 1976, *Shapiro et Elliott 471* (MICH, MO). Jalisco: Reserva Biosfera de la Sierra de Manantlán, 16 km by new dirt road WSW of El Terrero, 22 March 1989, *Cochrane, Wetter, et Cuevas G. 11730* (WIS); 12 km al NO de El Chino, camino a Nacastillo, 3 July 1981, *J. Magallanes 2959* (MO); steep rocky valley of Río Las Juntas, 10–13 km SE of El Tuito, altitude 250–300 m, 14–16 December 1970, *R. McVaugh 25393* (MICH). Nayarit: bank of Río Santiago, Tepic, 1 June, *J. Gregg 1043* (MO); 16 miles E of San Blas, 6 January 1973, *C. D. Johnson 109-73* (MO), 27 February 1973, *239-73* (MO). Oaxaca: 1 km E of Zacatepec on Mexico 190, 31 May 1980, *Seigler, Richardson, et Thompson 11582* (ILL); a 6 km al N de Sta. Ma. Zacatepec, Dist. Putla, 19 August 1976, *Sousa, Ramos, Téllez, et Rico 5863* (MO, Tex); a 5 km al NE de San Pedro Tapanatepec, Distr. Juchitán, 16 December 1978, *Sousa et Ricco 10157* (MEX); a 2 km al NW de Pinotepa Nacional, Distr. Jamiltepec, 27 June 1979, *Sousa, Sousa, Basurto, Grether, et Durán 10574* (MEX); Nejapa: a 5 km al S-SW de Santa María Zacatepec, Distr. Putla, 27 June 1979, *Sousa, Sousa, Basurto, Grether, et Durán 10587* (MEX).

BAT REPRODUCTION IN THE LUQUILLO EXPERIMENTAL FOREST OF PUERTO RICO

MICHAEL R. GANNON AND MICHAEL R. WILLIG

*Ecology Program, Department of Biological Sciences and The Museum,
Texas Tech University, Lubbock, TX 79409-3131*

*Present address of MRG: Department of Biology, The Pennsylvania State University,
3000 Iydside Park, Altoona, PA 16601*

Most detailed studies of bat reproduction concern temperate zone species (Cockrum, 1955; Brenner, 1968; Fenton, 1970; Madhavan, 1971; O'Farrell and Studier, 1973) or Old World tropical species (Mutere, 1967, 1970, 1973; Thomas and Marshall, 1984; Heidman, 1988, 1989). Nonetheless, patterns of reproduction in neo-

tropical bats have received increasing attention in recent years (Racey, 1982, 1988; Willig, 1985a, 1985b, 1985c; Fleming, 1988). Four basic reproductive patterns are known for neotropical bat populations: seasonal monestry, seasonal polyestry, seasonal bimodal polyestry, and aseasonal polyestry (Fleming et al., 1972; Wilson, 1973;

Willig, 1985a). Reproductive patterns appear to be geographically variable, particularly in phyllostomids (Wilson, 1979), and are likely regulated by abiotic variables (Wilson, 1979; Racey, 1982). Timing of birth in several tropical bats is known to vary with environmental factors including ambient temperature, photoperiod, and rainfall (Racey, 1982). In particular, rainfall appears to be the most important climatic factor affecting bat reproductive cycles in the tropics. It may act directly as the external cue initiating reproductive activity, or may have indirect effect on reproduction through regulation of phenology of both fruit-bearing plants and insects which serve as forage for bats (Heidman, 1988). Nonetheless, a diversity of patterns persists throughout the tropics. For example, in a number of seasonally breeding Old World bats, births occur just before the appearance of peaks in rainfall (Mutere, 1967, 1970, 1973; Thomas and Marshall, 1984). Phyllostomids in Costa Rica are cyclic and avoid parturition during the dry season (Mares and Wilson, 1971). In many neotropical species that annually produce two young, births coincide with maximum food levels at the end of the dry season and the middle of the rainy season (Fleming et al., 1972). Moreover, species in Panama, whose food sources remain abundant over most of the year and are not limited by rainfall, produce two litters annually (Bonaccorso, 1979). In contrast, in Colombia, where its food supply is abundant all year long, *Artibeus lituratus* breeds throughout the year (Tamsitt and Valdivieso, 1963, 1964). In semiarid northeastern Brazil, several phyllostomid frugivores (*Carollia perspicillata*, *Vampyrops lineatus*, *A. jamaicensis*, and *A. lituratus*) exhibit bimodal polyestry, with parturition and lactation concentrated during the rainy season, whereas the phyllostomid nectarivore, *Glossophaga soricina*, exploits pollen and nectar, as well as fruit, and thereby exhibits bimodal polyestry with a birth peak in both rainy and dry seasons (Willig, 1985a, 1985c). Taddei (1976) examined 16 species of phyllostomids from southeastern Brazil and found that they exhibited two birth peaks each year which correspond to rainy seasons.

The reproductive biology of Puerto Rican bats is poorly documented (Willig and Gannon, 1993). Although bats compose the major portion of the Puerto Rican mammalian fauna in terms of species' richness and density (Willig and Bauman, 1984; Willig and Gannon, 1993), and are Puerto

Rico's only indigenous mammals, most previous work has been limited to taxonomic description, specimen collection, or descriptive observation (Anthony, 1918, 1925; Tamsitt and Valdivieso, 1971). Here, we describe reproduction of *Stenoderma rufum*, *A. jamaicensis*, and *Monophyllus redmani*, the three most common bats in the Luquillo Experimental Forest of Puerto Rico. Additionally, we include sex ratios for males and females of each species in both the rainy and dry seasons.

Because of its limited range and rarity in scientific collections, little information has been published concerning *S. rufum*. Most previous reports on reproduction (Tamsitt and Valdivieso, 1966, 1971; Tamsitt, 1970; Jones et al., 1971; Genoways and Baker, 1972; Willig and Bauman, 1984) have been anecdotal and included observations on few individuals. Based on such information, Wilson (1979) suggested that *S. rufum* may be polyestrous, but noted that data are lacking to be confident of that conclusion. The reproductive biology of *A. jamaicensis* is much better known throughout its range and is characterized by geographic variation in reproductive patterns (Wilson, 1979). In Cuba, *A. jamaicensis* clearly exhibits bimodal polyestry with parturition peaks in March–April and July–August (Silva Taboada, 1979). In contrast to the detailed data from Cuba, few observations have been documented from Puerto Rico. Only one report (Buden, 1975) has documented any reproductive information on *M. redmani* and this work is based upon 10 individuals from various locations throughout the Greater Antilles (one of which is from Puerto Rico).

Field Studies—Bats were netted in the Luquillo Experimental Forest of Puerto Rico during 1988 and 1989. This forest zone is located on the lower slopes of the Luquillo Mountains and receives between 2,000 and 4,000 mm of rain annually. Although average monthly rainfall varies from a maximum in May of 460 mm to a minimum of 290 mm in January, seasonal differences in precipitation are not pronounced (McDowell and Estrada-Pinto, 1988). Each bat was identified to species, sexed, and weighed to the nearest 0.5 g. Males were considered reproductively active if testes were descended, or inactive if testes were not descended. Females were classified as pregnant (determined by abdominal palpation), lactating, pregnant and lactating, or inactive. All individuals were released after capture.

Museum Studies—Adult specimens (based upon

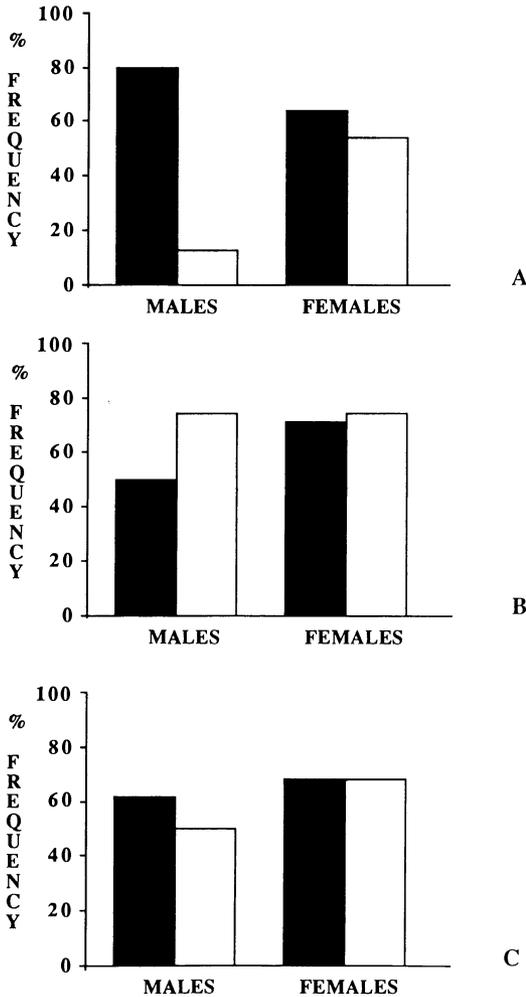


FIG. 1.—Frequency of adult male and female *S. rufum* in the rainy (open bars) and dry (solid bars) seasons that were reproductively active (males: testes descended; females: pregnant or lactating). A = museum specimens (males, $n = 33$; females, $n = 55$); B = live specimens (males, $n = 20$; females, $n = 35$); C = museum and live specimens combined.

ossification patterns of crania and phalanges) of *S. rufum* collected in the Luquillo Experimental Forest were obtained from The Museum of Texas Tech University, The Royal Ontario Museum, and Carnegie Museum of Natural History. When available, reproductive information for individuals preserved as dried skins was obtained from specimen tags and field notes. The majority of museum specimens examined was preserved in

fluid, with reproductive condition evaluated directly by necropsy. Both museum and field specimens were classified as to season (rainy or dry) of capture. In addition, crown-rump length of embryos obtained from fluid-preserved specimens was measured to estimate developmental stage.

For both *S. rufum* and *A. jamaicensis*, G-tests (Sokal and Rohlf, 1981) were used to compare patterns of reproductive activity in wet and dry seasons for males (percent testes descended versus not descended) and females (percent pregnant or lactating versus inactive) separately. Year to year variation in reproductive activity was compared in the same manner. Binomial tests (Sokal and Rohlf, 1981) were used to determine whether observed sex ratios differed significantly from 1:1.

Fifty-five adult *S. rufum*, 54 adult *A. jamaicensis*, and 19 adult *M. redmani* were captured in the Luquillo Experimental Forest during 1988 and 1989. Ninety-eight adult *S. rufum* were obtained from museums.

Reproductive Patterns—Although field (Fig. 1A) and museum (Fig. 1B) data for *S. rufum* suggested some differences in seasonality of male reproductive activity, no appreciable differences existed for females. When data were combined from both sources and analyzed statistically, no significant differences were detected in female reproductive activity between rainy (67.5% of 77 adult females pregnant or lactating) and dry (80.0% of 25 adult females pregnant or lactating) seasons (G-Test of independence: $G = 0.58$, $d.f. = 1$, $0.05 > P > 0.01$). Moreover, the same wide range of embryo sizes characterized both seasons (Fig. 2). Such a broad overlap in the frequency size distributions of embryos throughout the year indicates an extended period during which fertilization occurs (Mares and Wilson, 1971). The presence of simultaneously pregnant and lactating females ($n = 11$) suggests that *S. rufum* is polyestrous, but the polyestry is asynchronous in that pregnancy occurs throughout the year. Such asynchronous polyestry is characteristic of species whose food does not vary greatly in abundance on a seasonal basis (Wilson, 1979).

Observations in the Luquillo Experimental Forest suggest that fruit availability at this location is only slightly seasonal (as is precipitation) and that the major disseminator of most animal-dispersed fruits are bats (Devoe, 1990; Willig and Gannon, 1993). Still, observations that a large portion of the fruit crop falls to the ground with-

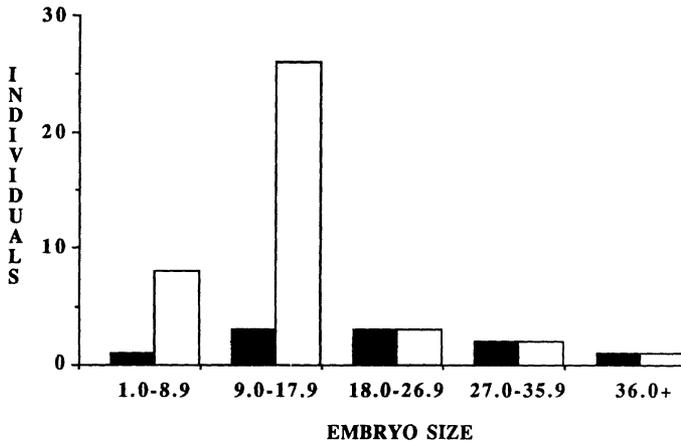


FIG. 2.—Distribution of embryo sizes (crown-rump length, in mm) in museum specimens of *S. rufum* for rainy (open bars, $n = 54$) and dry (solid bars, $n = 11$) seasons.

out being consumed suggests that the intensity of arboreal frugivory is low and indicates that excess fruit exists in ample supply year round (Devoe, 1990). For *S. rufum*, whose diet primarily comprises *Cecropia schreberiana*, *Mandilkara bidentata*, and *Prestoea montana* (Gannon, 1991; Willig and Gannon, 1993), there may be no seasonal energetic or nutritional constraints that result in seasonal modes of reproductive activity.

The results for *A. jamaicensis* (Table 1), when compared with data from Willig and Bauman (1984), demonstrate that the proportion of reproductively active females of this species during the rainy season is statistically variable (G-Test of Independence: $G = 6.16$, $d.f. = 2$, $0.025 > P > 0.01$) from year to year. Of 45 adult females,

68.8% were pregnant or lactating in 1982 (Willig and Bauman, 1984), whereas 36.6% ($n = 30$ adult females) were reproductively active in field samples from 1988 and 1989. In part, this difference may be due to methodology. The latter samples were based solely on field palpation of live females, which may underestimate true reproductive activity, whereas the 1982 data were based on necropsy. Few data exist for *A. jamaicensis* during the dry season in Puerto Rico. Two of 6 adult females were reproductively active during 1988 and 1989. These data do not suggest differences beyond the variation characteristic within a season.

Sex Ratios—Sex ratios of Puerto Rican bats from the Luquillo Experimental Forest have not

TABLE 1—Reproductive characteristics of bats in the Luquillo Experimental Forest during dry and rainy seasons. Total numbers are reported, followed by number breeding (in parentheses). Museum data are based upon specimens collected over a 20-year period. An asterisk (*) indicates a sex ratio that statistically differs from 1:1.

Species	Dry season				Rainy season			
	Male	Female	M:F	Percent breeding	Male	Female	M:F	Percent breeding
<i>Stenoderma rufum</i> ¹	5 (4)	11 (7)	1.0:2.2	69	15 (2)	24 (13)	1.0:1.6	38
<i>Stenoderma rufum</i> ²	8 (4)	14 (10)	1.0:1.8	64	23 (17)	53 (39)	1.0:2.3*	73
<i>Artibeus jamaicensis</i> ¹	12 (7)	6 (2)	2.0:1.0	50	16 (10)	30 (11)	1.0:1.9	64
<i>Monophyllus redmani</i> ¹	6 (2)	4 (1)	1.5:1.0	30	9 (2)	0 (0)	1.0:0.0*	19

¹ Field data (1988–89).

² Museum data.

been previously reported. Male to female sex ratios were calculated for museum and field samples (Table 1). Although females appear more abundant in both seasons for two species, results did not statistically differ from an equal sex ratio in most cases. Only museum data for *S. rufum* from the rainy season revealed a sex ratio highly skewed toward females (Binomial Test, $P < 0.001$). Field data for *M. redmani* in the rainy season (Binomial Test, $P < 0.004$) were also demonstrative of unequal sex ratios in that no females were captured in that season.

Sex ratios of neotropical bats appear to depend on locality, season, and age. For example, the sex ratio for *A. jamaicensis* in Costa Rica (Mares and Wilson, 1971) is female-biased. Willig (1983) also reported sex ratios of fifteen bat species from northeastern Brazil. Of 11 phyllostomids, six were female-biased, including *A. jamaicensis*, and five had equal sex ratios. Four non-phyllostomids had equal ratios. Silva Taboada (1979) found 1:1 ratios in adult *A. jamaicensis* on Cuba, as well as in four other phyllostomids and ten species of non-phyllostomids from the same location. Similar ratios were obtained for *A. jamaicensis* in Panama (Morrison, 1975). In Costa Rica, *Carollia perspicillata* exhibits a male-biased secondary sex ratio (birth), but in adults it was virtually 1:1 (Fleming, 1988).

Female-biased sex ratios may be a result of differential mortality rates between the sexes and between age groups, as appears to be the situation for *C. perspicillata*. However, behavior patterns may influence sex ratios as well. McNab (1963), Smith (1968), and Thomas (1972) suggest that the presence of greater numbers of females in a population sample may result from increased energy requirements of pregnant and lactating females. This would manifest itself in longer foraging bouts, larger home ranges, or both, and thus increase the likelihood of capture. It has been demonstrated for *S. rufum* that males and females in Puerto Rico exhibit similar home range sizes and foraging behavior (Gannon, 1991); however, these results were obtained only from reproductively inactive individuals.

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