

REPRODUCTIVE PATTERNS OF BATS FROM CAATINGAS AND CERRADO BIOMES IN NORTHEAST BRAZIL

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ABSTRACT.—Current ecological hypotheses suggest that annual reproductive patterns in tropical bats are related to rainfall such that individuals avoid weaning their young during the most stressful season of the year. The reproductive status of bats within well delineated populations from Caatingas and Cerrado biomes of Northeast Brazil were monitored over a 20-month period; seven species were captured in sufficient numbers to determine annual reproductive patterns with confidence. *Noctilio leporinus* exhibited seasonal monestry. *Glossophaga soricina*, *Carollia perspicillata*, *Vampyrops lineatus*, *Artibeus jamaicensis*, and *A. lituratus* exhibited seasonal bimodal polyestry. *Desmodus rotundus* exhibited asynchronous polyestry. Major differences were not detected between Caatingas and Cerrado populations of any species, even though the predictability and total amount of precipitation was different in the two biomes. Most species (*N. leporinus*, *V. lineatus*, *A. jamaicensis*, *A. lituratus*, *C. perspicillata*) wean their young primarily during the wet season, whereas *G. soricina* weans its first litter during the dry season and its second litter during the wet season.

Knowledge of bat population dynamics in tropical South America is quite limited. Information concerning bat reproduction is based primarily upon temperate zone species where, due to climatic restrictions, reproductive cycles are short in duration and presumed to be regulated by abiotic variables (Racey, 1982; Tuttle and Stevenson, 1982; Wilson, 1979). As a consequence, temperate bats are limited to one litter per year, with almost all species giving birth within a relatively short period of time (Kruttsch, 1975; Oxberry, 1979). Early surveys of neotropical bat reproduction (Anderson and Wimsatt, 1963; Tamsitt and Valdivieso, 1963, 1965; Wilson and Findley, 1970) provided the initial hypotheses concerning other reproductive patterns, but these studies produced insufficient data to generalize regarding the effects of latitude or precipitation patterns on reproduction. Work by Mares and Wilson (1971) indicated that, despite the apparent luxuriance of neotropical habitats, reproduction in Costa Rican phyllostomids appeared to be cyclic, avoiding reproduction during the harsh dry season. Additional data on phyllostomids from Panama (Fleming, 1973) and Costa Rica (Wilson, 1973) indicated bimodal reproduction. Birth peaks in phyllostomid reproductive activity occur progressively later in the year with increasing latitude from Colombia to Panama to Costa Rica; these shifts appear to be related to precipitation regimes and resource abundance.

Bats exhibit four basic reproductive strategies: aseasonal polyestry, seasonal polyestry, seasonal bimodal polyestry, and seasonal monestry (Carter, 1970; Fleming et al., 1972; Wilson, 1973). All of the patterns are ostensibly related to the seasonality of food resources (Wilson, 1973, 1979). At present, very few South American bat reproductive cycles are known and even less is known about the reproductive cycles of conspecific bat populations occupying different habitats. A notable exception is the detailed work of Myers (1977) in which vespertilionid reproduction patterns in arid Chacoan habitats were not found to be different from the patterns obtained in more mesic eastern Paraguayan habitats. Adequate information concerning phyllostomid reproductive patterns is available for only 20 bat species representing 11 genera (Wilson, 1979). Several of these patterns are inferred from minimal data pooled from different years and habitats. The recent summaries by Racey (1982) and Tuttle and Stevenson (1982) stress *lability* in bat reproduction over time and space for single species and indicate the importance of comparative studies. Research reported herein examines the reproductive patterns exhibited by female bats in two distinct biomes of Northeast Brazil. Although, in general, Caatingas and

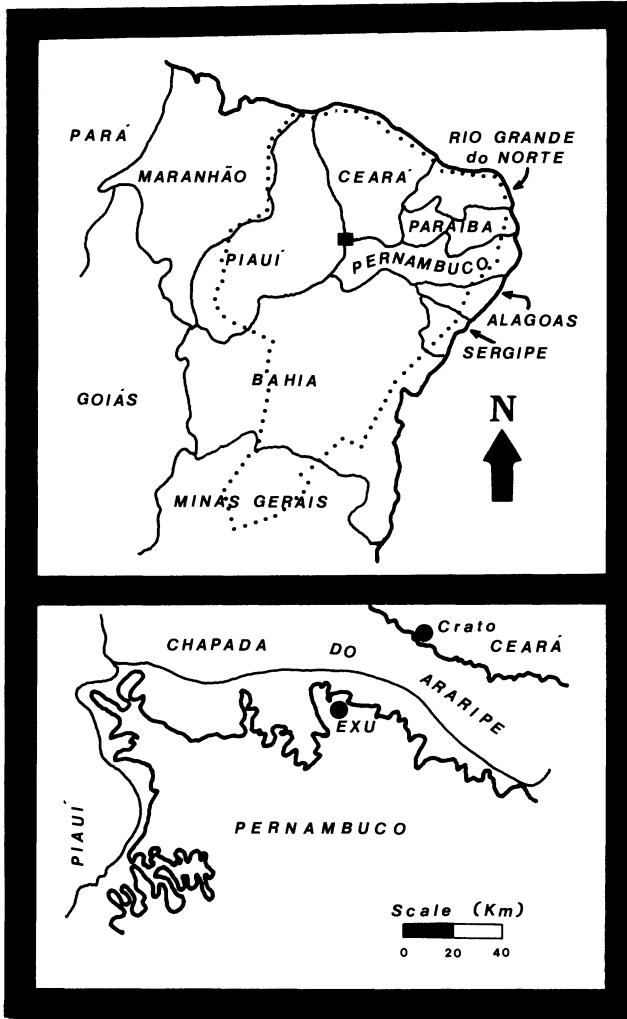


FIG. 1.—The Caatingas, delimited by the dotted line, is contained within the nine states of the Brazilian Northeast [above]; because of its irregular shape and susceptibility to extended xeric periods, the region is known as the polygon of drought. The solid rectangle indicates the location of the Caatingas (Exu, Pernambuco) and Cerrado (Crato, Ceará) study sites. The proximity of the study sites, and their relation to the Chapada do Araripe are indicated on the lower portion of the map.

Cerrado biomes differ in the predictability of rainfall and in total precipitation in the Exu-Crato area, they are similar in terms of seasonality. One would, therefore, expect Caatingas and Cerrado populations of the same species to exhibit similar reproductive patterns if species are adapted to the long-term average occurrence of precipitation. Conversely, Caatingas populations might exhibit less synchrony and/or more variability than Cerrado populations if the proximate factors which elicit the initiation of reproductive activity are correlated with the observed precipitation during a particular year.

Northeastern Brazil is dominated by a large heterogeneous semiarid region known as the Caatingas (Fig. 1). It extends between 35° and 45° W and 3° and 16° S (Reis, 1976), and occupies $650,000 \text{ km}^2$ (Frota-Pessoa et al., 1971). In general, extreme spatial and temporal climatic

variability characterize the region (Markham, 1972; Markham and McLain, 1977; Melo, 1956), with the distribution and quantity of rainfall being affected by complex interrelationships among the Southeast Trade Winds; three large, mobile, moisture-laden air masses (i.e., the equatorial continental mass, the Atlantic Polar Front, and the Intertropical Convergence Zone); and an irregular pattern of orographic barriers (Markham, 1972; Reis, 1976). The distinctive topographic relief of the Caatingas is a product of three major geological components: a pervasive pre-Cambrian crystalline basement that produces extensive flatlands; granitic protrusions that form mountains (serrotes) and low-land outcroppings (lajeiros); and the original sandstone substrate that forms large plateaus (chapadas) in areas unaffected by post-Cretaceous erosion (Ab'Sáber, 1970; James, 1942). As a result of these topographic and climatic attributes, the Caatingas supports a number of distinct habitats: caatinga baixa in low-lying areas; caatinga alta on the slopes of serrotes; lajeiros; and edaphic forms of cerrado and cerrado vegetation on chapadas (Mares et al., 1981; Mares et al., 1985; Streilein, 1982; Willig, 1983).

METHODS

This research was concentrated in the geographic center of the Northeast in order to examine the bat fauna in each of the Caatingas habitats. Field work was equally divided between the municipality of Exu, Pernambuco, and the adjacent municipality of Crato, Ceará, in the Floresta Nacional Araripe-Apodí. The Exu site, located at the leeward base of the Chapada do Araripe, contained a xerophytic assemblage of plants discussed extensively by Mares et al. (1981), Streilein (1982), and Willig (1983). Lajeiros, serrotes, caatinga alta, and caatinga baixa habitats greatly interdigitate and are in very close proximity in the Exu area, and are best considered components of a heterogeneous Caatingas biome. In contrast, the contiguous savanna-like cerrado and cerrado habitats of the windward half of the Chapada do Araripe together constitute a distinct edaphic formation (Cerrado biome) in terms of floral composition, physiognomy, and geomorphology, which is spatially disjunct from the Caatingas biome (Mares et al., 1981; Willig, 1983). Hence, the geographic area known as the Caatingas encompasses both an open-forest savanna formation (Cerrado biome) and a deciduous drought-adapted formation (Caatingas biome). The paleoecology and biogeography of the region are further discussed by Mares et al. (1985).

Long-term climatic regimes for both biomes exhibit a similar pattern of rainfall, with the wet season extending from approximately November–December until April–May. However, the Caatingas experiences large yearly fluctuations in rainfall, while the levels of precipitation on the Chapada do Araripe are more consistent from year to year. In addition, the total precipitation on the Chapada do Araripe, in the vicinity of Crato, Ceará, is greater than in Caatingas habitats of the Exu area. Detailed meteorological summaries for the Northeast are provided by Reis (1976) and Streilein (1982).

Bats were collected by netting from September, 1976 to May, 1978 in both Caatingas (Exu, Pernambuco) and Cerrado (Crato, Ceará) biomes. Because I was interested in determining the reproductive patterns of well-delimited chiropteran populations within both Caatingas and Cerrado biomes, monthly samples within a restricted geographic area were utilized in subsequent analyses. Sampling locales were contained within a circular area whose radius was 10 km in each biome; 5 to 10 locales within that area were sampled each month. Standard Japanese mist nets were used to collect most specimens; however, supplemental collections from roosts (e.g., caves, tree hollows, buildings, culverts) augmented the samples.

Shortly after capture, specimens were either sacrificed or marked and released. Age (adult or juvenile), sex, and reproductive condition (males: testes descended or not descended; females: pregnant, lactating, or inactive) were noted for all captured individuals. Only the most abundant species were involved in the mark-release program, and then only after at least five males and five females had been previously collected from that month and biome.

Sacrificed specimens were processed in two different ways. Most frequently, standard museum skins and skulls were prepared, with the reproductive organs preserved in FAA (formalin, ethyl alcohol, and acetic acid). At other times, specimens were preserved in 10% formalin, with FAA injected into the abdominal cavity. The preserved reproductive tracts of females were later examined to reveal any initial stages of pregnancy that may have been undetected by field palpation techniques. Samples from the same month in different years were not pooled so as to avoid concealing annual differences in reproduction, which could be related to annual differences in precipitation regimes and/or resource abundance.

RESULTS AND DISCUSSION

Two factors, both subject to natural selection, affect the observed reproductive pattern of a population. The number of births that an individual can execute successfully in a year deter-

TABLE 1.—Bat species composition of Caatingas and edaphic Cerrado habitats of Northeast Brazil. Relative abundance categories: A = abundant; C = common; R = rare; — = absent.

Species	Abundance	
	Caatingas	Cerrado
<i>Saccopteryx leptura</i>	—	R
<i>Peropteryx macrotis</i>	C**	—
<i>Noctilio leporinus</i>	C*	R
<i>Pteronotus davyi</i>	R	R**
<i>Micronycteris megalotis</i>	R-C**	R
<i>Micronycteris minuta</i>	R-C**	R
<i>Tonatia bidens</i>	R**	—
<i>Tonatia brasiliense</i>	R-C**	—
<i>Tonatia silvicola</i>	C**	—
<i>Mimon crenulatum</i>	R-C**	—
<i>Phyllostomus discolor</i>	R-C**	A**
<i>Phyllostomus hastatus</i>	R**	A**
<i>Trachops cirrhosus</i>	C**	—
<i>Glossophaga soricina</i>	A*	A*
<i>Lonchophylla mordax</i>	C**	—
<i>Anoura geoffroyi</i>	R**	C**
<i>Carollia perspicillata</i>	A*	A*
<i>Sturnira lilium</i>	R**	R-C**
<i>Uroderma magnirostrum</i>	R**	R**
<i>Vampyrops lineatus</i>	A*	A*
<i>Artibeus concolor</i>	—	R-C**
<i>Artibeus jamaicensis</i>	C*	A*
<i>Artibeus lituratus</i>	C-R**	A*
<i>Desmodus rotundus</i>	A*	R**
<i>Diphylla ecaudata</i>	R**	—
<i>Natalus stramineus</i>	—	R
<i>Furipterus horrens</i>	R**	—
<i>Myotis nigricans</i>	C-A**	C**
<i>Eptesicus furinalis</i>	—	R-C**
<i>Lasturus borealis</i>	—	R**
<i>Lasturus ega</i>	R**	R**
<i>Molossops planirostris</i>	R**	—
<i>Molossops temminckii</i>	R**	R
<i>Tadarida laticaudata</i>	R	R
<i>Neoplaticomys mattogrossensis</i>	C***	—
<i>Molossus ater</i>	R	—
<i>Molossus molossus</i>	A**	A*
<i>Eumops</i> sp.	R	—

* Reproductive patterns described in text.

** Reproductive activity described by Willig (1985b).

*** Reproductive activity described by Willig (1985a).

mines the potential modality of a population's reproductive cycle, while the degree of synchrony among all individuals in a population determines, in effect, the realization of a particular pattern. Synchronous monestry or polyestry result in seasonality; in fact, the existence of seasonal resource abundance is presumably the primary agent that would select for reproductive synchrony in a population. Other combinations of synchrony and estrous cycle potentially could yield seasonal population peaks in reproduction (e.g., two subsets of a population that display intragroup synchrony but intergroup asynchrony in parturition would yield a bimodal pattern of births); however, these have not been observed in the field and the selective processes that might lead to them remain obscure. Asynchrony in a monestrous or polyestrous species results in an acyclic population pattern of continuous reproduction which would be particularly adaptive in areas where requisite resources were available in adequate supply year-round. Synchrony may be incomplete, and some individuals in a population may not maintain an embryo to parturition. Any combination of these two situations could obscure the resolution of reproductive patterns in a population.

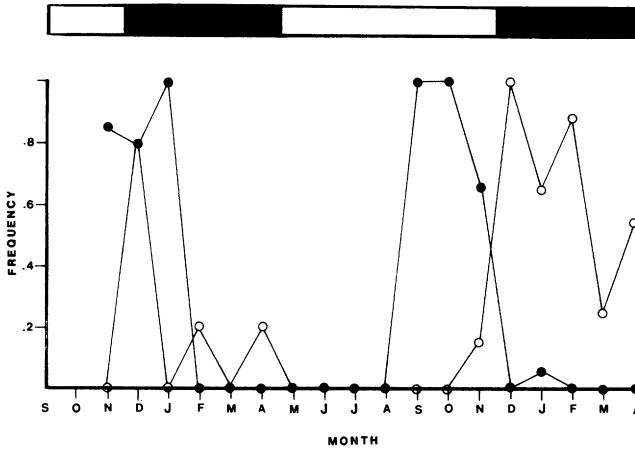


FIG. 2.—Reproductive pattern of female *Noctilio leporinus* in the Caatingas biome. Solid circles indicate the monthly proportion of adult females that are pregnant; open circles indicate the monthly proportion that are lactating. The horizontal bar defines the precipitation regime of the area based upon records of mean monthly temperature and total monthly rainfall for a 14-year period (September, 1964 to July, 1978). Shaded portions of the bar represent periods of water surplus (wet season) and unshaded portions represent times of water deficit (dry season). Monthly sample sizes are available in Appendix 1.

The absence of unbiased statistical methods for determining the number of peaks in a reproductive cycle is problematic and will probably remain so until long-term studies of reproduction over many years allow the application of time-series analyses. In practice, a number of population patterns of reproduction have been distinguished (Carter, 1970; Fleming et al., 1972; Tuttle and Stevenson, 1982; Wilson 1973, 1979). Seasonal monestry is indicated by a single peak in pregnancy followed by a lactation peak. Individuals are not found to be simultaneously pregnant and lactating in the middle of the pregnancy peak. A period of several months with complete reproductive inactivity frequently occurs. Seasonal bimodal polyestry is indicated by a bimodal distribution in pregnancy with a delayed bimodal distribution of lactation. During the second pregnancy peak, individuals may be simultaneously lactating and pregnant. If synchrony is not absolute within a population, the double peak in pregnancies may be obscured; however, the presence of simultaneously lactating and pregnant specimens halfway through the breeding season is a strong indication of bimodality. Seasonal polyestry is characterized by multiple peaks (three or more, to distinguish it from seasonal bimodal polyestry) in pregnancy and lactation; it is otherwise similar to seasonal bimodal polyestry. Aseasonal polyestry is indicated by the absence of distinct birth and lactation peaks; pregnant, lactating, and simultaneously lactating and pregnant individuals should be observed each month.

Over 5,000 specimens, representing 38 species, 29 genera, and 8 families, were captured from the Exu-Crato area (Willig, 1982, 1983). Females of seven species were consistently captured in adequate numbers to ascertain annual reproductive patterns with confidence. Monthly sample sizes for each species' population appear in Appendix 1. An accurate annual pattern could not be constructed for the other 31 species (Table 1) because samples were either too small or temporally restricted; however, summary reproductive data is included in another work (Willig, 1985b).

Noctilio leporinus.—Although Carter (1970) suggested that *N. leporinus* was polyestrous, Hooper and Brown (1968) showed that it exhibited a well-defined breeding season with a single population birth peak. Based upon a sample of 176 adult females, *N. leporinus* clearly exhibited seasonal monestry (Fig. 2) in the Caatingas biome. Pregnancies occurred from September until January, with juveniles appearing for the first time in January. Since many of the individuals

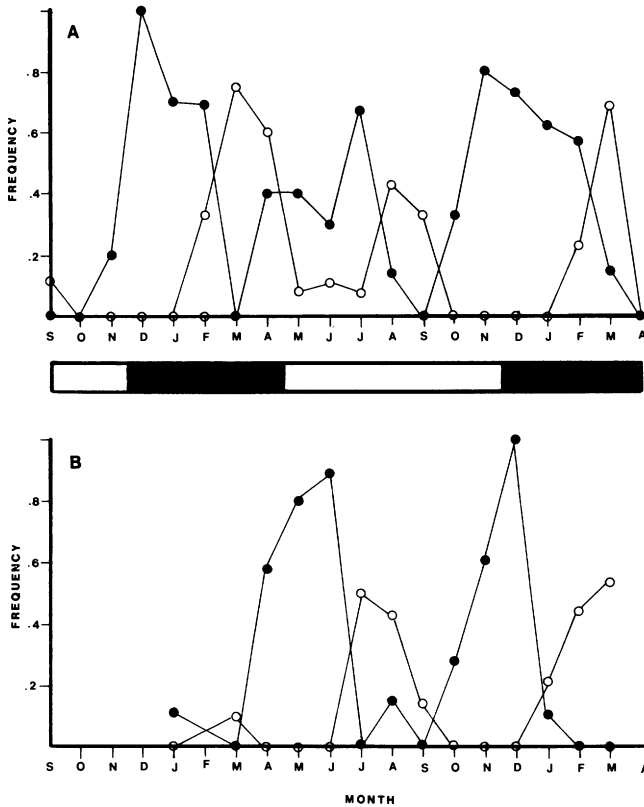


FIG. 3.—Reproductive pattern of female *Glossophaga soricina* in the Caatingas (A) and Cerrado (B) biomes of Northeast Brazil. Symbols as in Fig. 2. Monthly sample sizes for each biome are available in Appendix 1.

included in this summary of reproductive activity were involved in a mark-release study, field palpation was used to determine reproductive status in many cases. Thus, early stages of pregnancy may have been slightly underestimated. Lactation began as early as November and continued until April. May, June, and July were months of reproductive inactivity; during this time, females were neither pregnant nor lactating. Major energetic demands on the female (presumably, the latter stages of gestation and lactation) were restricted to the wet season, during which time both insect and small fish densities (observed in stomach contents during this study) were apparently greatest.

Glossophaga soricina.—Many authors have reported reproductive information for *G. soricina* (see Wilson, 1979), but most of the work has been restricted to Mexico, Central America, and northwestern South America. Rasweiler (1972) has shown that *G. soricina* is polyestrous in captivity, and field investigations have suggested that both acyclic polyestry (Cockrum, 1955; Felton, 1956; Tamsitt, 1966) and seasonal bimodal polyestry (Fleming, 1973; Heithaus et al., 1975) characterize local populations. Taddei (1973), in an exceptionally detailed account of phyllostomid reproductive patterns in northwestern São Paulo, suggested that his data conform to the pattern obtained by Cockrum (1955) and Tamsitt (1966). A close examination of the pattern in São Paulo revealed that a protracted period of pregnancies extended from June to February, with peak frequencies in August and in November. Two distinct lactation peaks existed. The first peak occurred from September until December and the second peak persisted

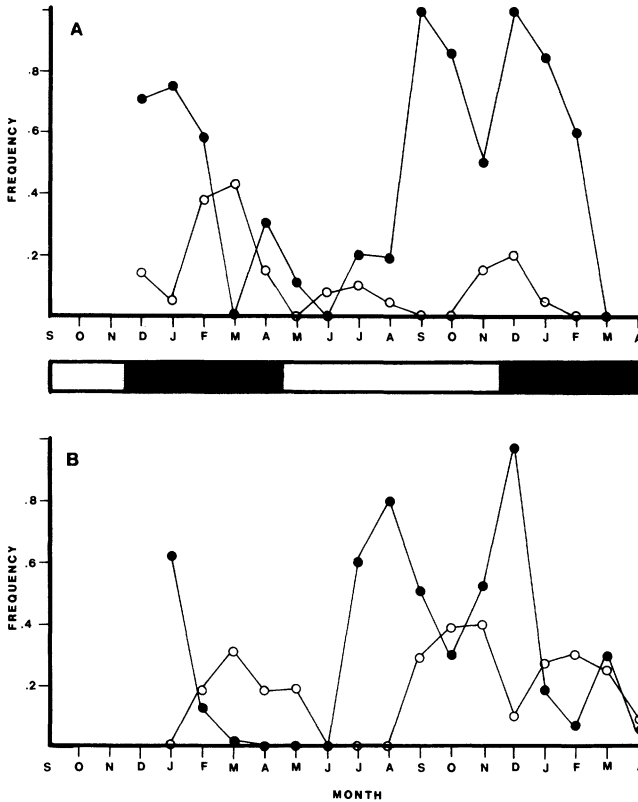


FIG. 4.—Reproductive pattern of female *Carollia perspicillata* in the Caatingas (A) and Cerrado (B) biomes of Northeast Brazil. Symbols as in Fig. 2. Monthly sample sizes for each biome are available in Appendix 1.

from February until May. The pregnancy peak preceded the lactation maxima by 3 months. A bimodal cycle was further suggested by the predominance of initial stages of pregnancy at the beginning of each peak. Although evidence of reproductive activity (pregnant and/or lactating females) was present in all months, reproduction was neither acyclic nor continuous in southwestern São Paulo.

The annual reproductive pattern of populations from Caatingas and Cerrado biomes ($n = 228$ and 223 adult females, respectively) did not differ substantially (Fig. 3). Both Northeast populations exhibited seasonal bimodal polyestry, with birth and lactation concentrated in the middle of the dry season and the mid- to late wet season. Pregnancy peaks occurred from April to July and from October to February. Unlike the other 4 phyllostomids, very few individuals (less than 1% in each biome) were pregnant while lactating. As in the case of *G. soricina* in northwestern São Paulo, the initiation of lactation in Northeast populations lagged behind the initiation of pregnancy by approximately three months. Unlike the São Paulo population, which exhibited lactation maxima at the interfaces between wet and dry seasons, Northeast populations exhibited lactation peaks in the middle of the dry season and at the end of the wet season.

Carollia perspicillata.—Data collated by Wilson (1979), as well as the work of Taddei (1973), support the contention of Fleming (1973) and Heithaus et al. (1975) that *C. perspicillata* exhibits seasonal bimodal polyestry with birth peaks occurring during the mid- to late dry season as well as in the middle of the wet season (before the heaviest rains begin).

Similarly, the Cerrado population from the Chapada do Araripe clearly exhibited seasonal

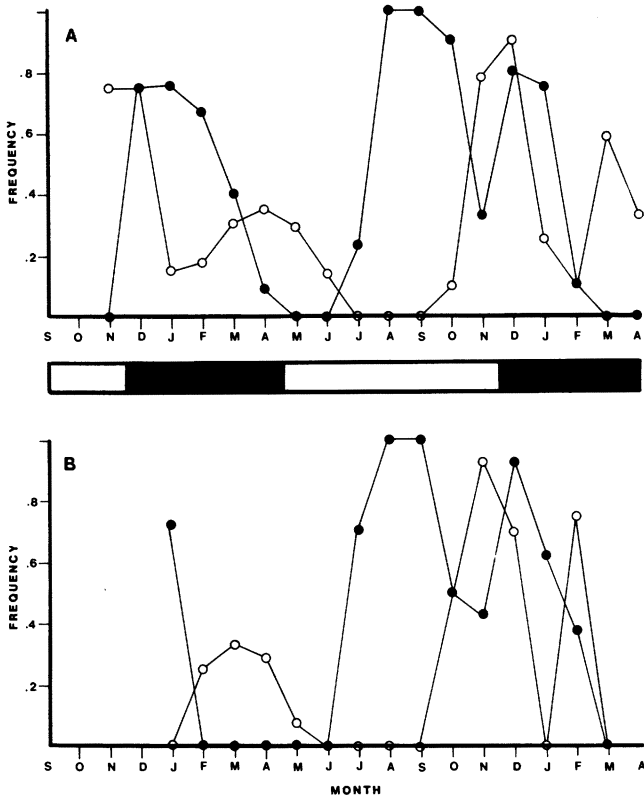


FIG. 5.—Reproductive pattern of female *Vampyrops lineatus* in Caatingas (A) and Cerrado (B) biomes of Northeast Brazil. Symbols as in Fig. 2. Monthly sample sizes for each biome are available in Appendix 1.

bimodal polyestry (Fig. 4B, $n = 444$ adult females). Two pregnancy peaks existed, the first from July to October and the second from October to January. Lactation peaks were out of phase by approximately two months. A substantial portion of the pregnant females were simultaneously lactating during the second pregnancy peak. The Caatingas population also had a bimodal cycle of pregnancy and lactation (Fig. 4A, $n = 193$ adult females); however, the occurrence of pregnancies in all months except June indicated that, like populations of *C. subrufra* (Wilson, 1979), at least a small portion of the Caatingas population may breed continuously or that complete synchrony is not characteristic of the population.

Vampyrops lineatus.—The reproductive biology of *V. lineatus* has not been well documented. Peracchi and Albuquerque (1971) reported the occurrence of pregnant females during December, January, and March in the Brazilian state of Rio de Janeiro. In a more detailed study from northwestern São Paulo, Taddei (1973, 1976) observed pregnant *V. lineatus* in all months except April. Lactating specimens appeared from November until May. There seemed to be a protracted period of reproductive activity for *V. lineatus*, with polyestry indicated by the presence of simultaneously pregnant and lactating females in November and December. The apparent absence of a well-defined breeding cycle may, at least in part, be attributed to small samples and the pooling of data that were collected over a seven-year period from 1967 to 1972.

The annual reproductive cycles of Caatingas and Cerrado populations were similar (Fig. 5, $n = 160$ adult females from Exu and 206 females from the Floresta Nacional Araripe-Apodí). An extended period of pregnancy commenced early in the dry season (July) and terminated early in the rainy season (February–March). A bimodal distribution of pregnancies occurred

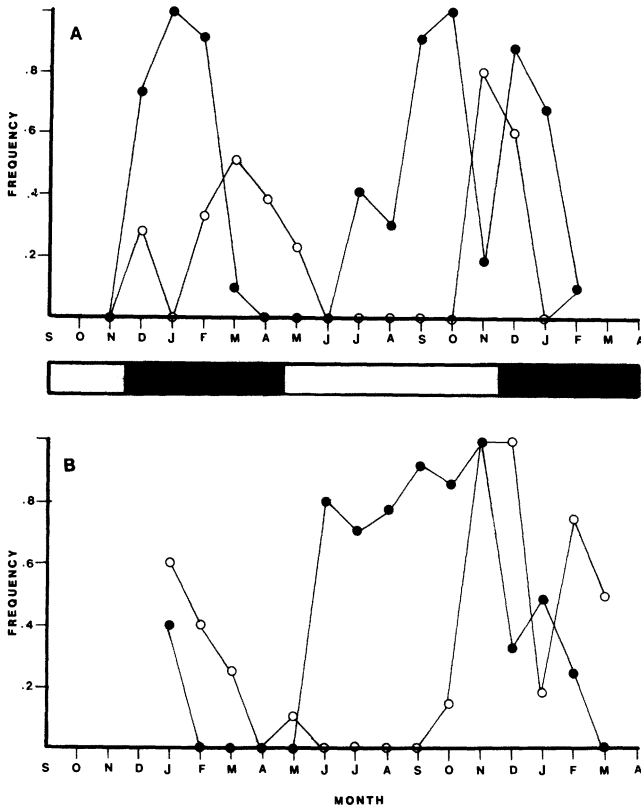


FIG. 6.—Reproductive pattern of female *Artibeus jamaicensis* in Caatingas (A) and Cerrado (B) biomes of Northeast Brazil. Symbols as in Fig. 2. Monthly sample sizes for each biome are available in Appendix 1.

within this period, while the incidence of lactation rapidly increased to approximately 90% during the second pregnancy peak. By the end of the rainy season, pregnancies ceased. *Vampyrops lineatus* clearly exhibited bimodal polyestry in both Caatingas and Cerrado biomes.

Artibeus jamaicensis.—The data summarized by Wilson (1979) on the reproductive biology of phyllostomids suggest geographically variable reproductive patterns for *A. jamaicensis*. Activity was synchronized in some localities (August and Baker, 1982; Felton, 1956; Goodwin, 1970; Tamsitt and Mejia, 1962) and acyclic in others (Jones et al., 1973; Tamsitt, 1966). The works of Bonaccorso (1979), Fleming (1971), and Fleming et al. (1972) indicate that *A. jamaicensis* is seasonally polyestrous (bimodal) in Panama with delayed development of blastocysts occurring after the second parturition peak. A paucity of data is available concerning reproductive activity for South American populations east of the Andes (Wilson, 1979). Peracchi and Albuquerque (1971) provided some records of reproductive activity in *A. jamaicensis* from Brazil, but more detailed information is available in the work of Taddei (1973, 1976). In the Brazilian Northeast, pregnant individuals occurred in all months with samples of three or more females, while lactation was restricted to the wet season and early dry season (November to May). Because females were often lactating and pregnant, polyestry is suggested; however, evidence for synchronous bimodality was lacking from northwestern São Paulo.

Caatingas ($n = 247$ adult females) and Cerrado ($n = 180$ adult females) populations exhibited essentially coincident reproductive patterns (Fig. 6). An extended bimodal frequency peak commenced in June or July and continued until March. The first lactation peak occurred from

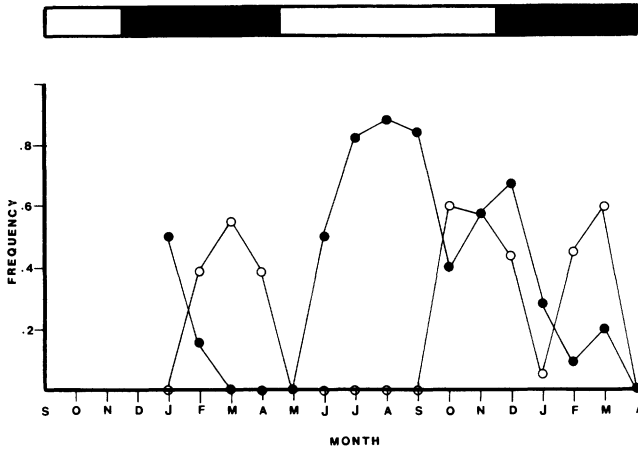


FIG. 7.—Reproductive pattern of female *Artibeus lituratus* in the Cerrado biome of Northeast Brazil. Symbols as in Fig. 2. Monthly sample sizes are available in Appendix 1.

October to December; juveniles appeared for the first time, independent from their mothers, in December–January. The second lactation peak attained a maximum between January and March, with second litter juveniles appearing in March.

Artibeus lituratus.—Extensive data have been reported on reproductive patterns in *A. lituratus*. Wilson (1979) suggested that these patterns are geographically variable, ranging from monestry at the northern limit of the range to bimodal polyestry (Thomas, 1972) or continuous acyclic breeding (Tamsitt and Valdivieso, 1963, 1965; Tamsitt, 1966) in Colombia. A few observations on the reproductive status of *A. lituratus* have been reported for Brazil by Peracchi and Albuquerque (1971) and Wilson (1979). Taddei (1973, 1976) presented the most detailed documentation of reproductive patterns; however, he did not detect a well-defined sexual season (although bimodality is suggested). This situation may be attributed to an extended period of parturition or to small monthly samples pooled for a seven-year period.

Samples from the Cerrado biome ($n = 193$ adult females) showed that *A. lituratus* exhibited seasonal bimodal polyestry (Fig. 7). Samples from the Caatingas biome were too small or temporally restricted to demonstrate a pattern for that biome; however, the available data (Willig, 1982) did not conflict with the pattern on the Chapada do Araripe. The first pregnancy peak persisted from June until October; the second peak continued from October to March. Lactation peaks proceeded from October to December and from February to April. Thus, the maximum energetic demands of reproduction occurred at the interface between wet and dry seasons and at the end of the wet season. This is quite similar to the pattern obtained by Bonaccorso (1979) for *A. lituratus* on Barro Colorado Island.

Desmodus rotundus.—The reproductive biology of this species is well documented (Wilson, 1979). All authors agree with the original interpretation by DeVerteul and Urich (1936) that *D. rotundus* breeds year-round. Data from a single population in the Caatingas ($n = 206$ adult females) were in agreement with the acyclic breeding model (Fig. 8). Pregnant, lactating, and simultaneously pregnant and lactating females occurred in all months with sample sizes greater than five individuals. Neither a cyclic pattern nor a period of inactivity were discernable.

SUMMARY

The idea that an organism maximizes its fitness is a paradigm in evolutionary biology. Parental strategies should involve a balance between maximizing individual survivorship (and therefore the potential number of litters per lifetime) and maximizing the number of progeny per litter which survive to reproduce. A given survivorship schedule results in an optimum litter size,

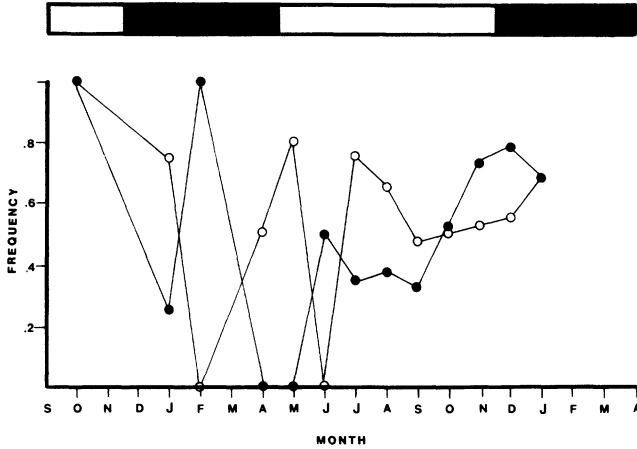


FIG. 8.—Reproductive pattern of female *Desmodus rotundus* in the Caatingas biome of Northeast Brazil. Symbols as in Fig. 2. Monthly sample sizes are available in Appendix 1.

which may be less than the potential maximum. The cost of reduced fertility per season is offset by increased survivorship to future reproductive seasons, as well as by increased juvenile survivorship. Bats in the families considered in this work (Phyllostomidae and Noctilionidae) seem to have evolved strong (genetic) constraints upon litter size; regardless of environmental conditions, individuals are monotoxic (although twinning occurs infrequently in some phyllostomid species). Hence, natural selection primarily operates on two demographic parameters: number of litters per year and yearly survivorship. Resource availability in terms of energy and nutrients is obviously a paramount constraint on both characteristics. It is not surprising, therefore, to see reproductive strategy intimately associated with foraging mode in bats. Parturition should occur at times of relative environmental beneficence because the demands of lactation are extremely costly in terms of maternal time and energy (Jenness and Studier, 1976; Miguela, 1969; O'Farrell and Studier, 1973; Studier et al., 1973).

In accord with the observations of Wilson (1979), reproductive patterns in bats from the Brazilian Northeast are related to rainfall patterns (Fig. 9); in addition, species exhibiting similar feeding modes exhibit parallel reproductive strategies. *Carollia perspicillata*, *V. lineatus*, *A. jamaicensis*, and *A. lituratus*, all phyllostomid frugivores, exhibit seasonal bimodal polyestry with parturition and lactation concentrated during the wet season, when fruit abundance and diversity is highest (see Willig, 1982). In contrast, *G. soricina*, a phyllostomid nectarivore, exhibits seasonal bimodal polyestry with one parturition/lactation peak at the end of the wet season and another during the dry season. The ability of *G. soricina* to exploit pollen and nectar in addition to fruit probably facilitates the expansion of the breeding season into months of the dry season which would be resource limiting for more stenophagic species. *Desmodus rotundus*, although a highly specialized sanguinivore, exploits resources (domesticated animals) which are in year-round abundance in the Northeast. As a consequence, reproduction is acyclic and continuous. *Noctilio leporinus*, a piscivore, exhibits seasonal monestry with parturition and lactation restricted to the wet season when insect and small fish populations reach the highest diversity and abundance.

The timing of reproduction in this study and others (e.g., Bonaccorso, 1979; Fleming et al., 1972; Humphrey and Bonaccorso, 1979) is related to resource abundance and does not seem to be affected by the predictability of precipitation. However, rainfall may indirectly mold reproductive patterns by affecting the timing of fruiting, flowering, and insect emergence. In addition, precipitation may act as a proximate cue for the initiation of reproductive cycles. Despite the differences in the predictability and total quantity of rainfall in Caatingas and Cerrado biomes,

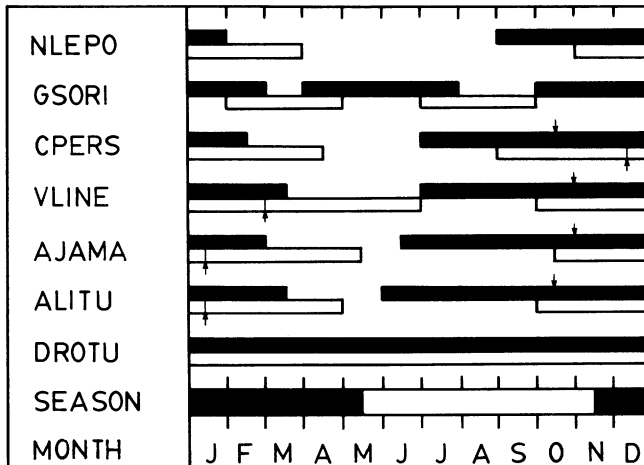


FIG. 9.—A comparison of generalized reproductive patterns in bats from the Brazilian Northeast. Solid horizontal bars represent the occurrence of pregnant females in the population; open horizontal bars represent the time of parturition and lactation. Vertical arrows define the transition between activity peaks in bimodal species. Species acronyms: NLEPO = *Noctilio leporinus*; GSORI = *Glossophaga soricina*; CPERS = *Carollia perspicillata*; VLINE = *Vampyrops lineatus*; AJAMA = *Artibeus jamaicensis*; ALITU = *Artibeus lituratus*; DROTU = *Desmodus rotundus*. The wet season is indicated by dark shading above months exhibiting a water surplus.

reproductive patterns for the species considered herein are quite similar. The long-term pattern of rainfall seems to be the dominant factor molding chiropteran reproductive strategies.

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APPENDIX 1.—Monthly sample sizes for females from Caatingas and Cerrado bat populations.

Time period*		<i>N. leporinus</i>		<i>G. soricina</i>		<i>C. perspicillata</i>		<i>V. lineatus</i>		<i>A. jamaicensis</i>		<i>A. lituratus</i>		<i>D. rotundus</i>	
		Caatingas	Cerrado	Caatingas	Cerrado	Caatingas	Cerrado	Caatingas	Cerrado	Caatingas	Cerrado	Caatingas	Cerrado	Caatingas	Cerrado
September	1976	0	6	—	0	—	0	—	0	—	—	—	—	—	0
October	1976	0	4	—	0	—	0	—	0	—	—	—	—	—	2
November	1976	7	5	—	0	—	4	—	4	—	1	—	—	—	0
December	1976	5	2	—	7	—	8	—	11	—	—	—	—	—	0
January	1977	2	7	71	16	11	13	11	3	5	6	6	4	4	4
February	1977	10	3	0	19	22	6	4	12	5	37	1	1	1	1
March	1977	4	4	9	14	59	10	6	21	8	22	0	0	0	0
April	1977	10	5	7	13	33	11	7	8	1	8	2	2	2	2
May	1977	8	25	10	17	16	7	13	13	9	3	5	5	5	5
June	1977	12	17	9	14	12	7	9	12	5	8	2	2	2	2
July	1977	4	12	4	10	5	4	14	17	7	6	55	55	55	55
August	1977	2	14	7	21	15	10	30	14	13	8	41	41	41	41
September	1977	32	31	7	9	35	9	38	22	65	19	30	30	30	30
October	1977	8	6	25	7	23	10	8	31	7	5	34	34	34	34
November	1977	6	10	23	6	47	18	14	39	5	7	15	15	15	15
December	1977	5	12	6	15	35	10	30	30	3	18	9	9	9	9
January	1978	17	13	9	19	44	4	13	3	41	18	6	6	6	6
February	1978	8	21	25	5	41	9	8	10	4	22	0	0	0	0
March	1978	20	18	11	1	24	14	1	0	2	5	0	0	0	0
April	1978	16	13	0	0	22	6	0	0	0	1	0	0	0	0
Total		176	228	223	193	444	160	206	247	180	193	206	206	206	206

* Netting was not begun in edaphic Cerrado habitats until 1977; hence, a dash (—) appears for September through December, 1976. Extensive netting was discontinued in both areas in April, 1978.