



Reproductive phenologies of phyllostomid bat populations and ensembles from lowland Amazonia

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Natural selection should favor individuals that synchronize energy-demanding aspects of reproductive activity with periods of high resource abundance and predictability, leading to seasonal patterns of reproduction at the population level. Nonetheless, few studies—especially those on bats in the Neotropics—have used rigorous quantitative criteria to distinguish among phenological patterns for different populations from the same habitat or for the same species in different habitats. To explore such issues, we quantified annual patterns of reproduction in male and in female bats from lowland Amazonia (environs of Iquitos, Peru), and did so at the level of populations and ensembles. Five species exhibited unimodal patterns including *Artibeus obscurus*, *A. planirostris*, *Carollia benkeithi*, *Phyllostomus hastatus*, and *Rhinophylla pumilio*. Two species (*A. lituratus* and *Glossophaga soricina*) evinced bimodal patterns with reproductive peaks separated by patterns of inactivity, whereas four species (*C. brevicauda*, *C. perspicillata*, *Sturnira lilium*, and *S. tildae*) evinced a bimodal pattern in which peaks in activity occur in tandem, with the first peak generally markedly higher than the second peak. Frugivore, gleaning animalivore, and nectarivore ensembles exhibited bimodal, unimodal, and bimodal reproductive phenologies, respectively. Nonetheless, interannual variation in phenology (i.e., the monthly timing of peaks within a season rather than the number of peaks per year) characterized four (*A. obscurus*, *C. brevicauda*, *C. perspicillata*, and *S. lilium*) of the eight species and each of the three ensembles (frugivores, gleaning animalivores, and nectarivores) with adequate sampling. Regardless of interspecific variation in strategies, the phenology of reproduction enhances the likelihood that parturition and recruitment of young into the population occurs during the wet season, the period of likely highest resource abundance. Based on a comparison of our results with those from other well-studied bat populations, four species did not exhibit geographic variation in reproductive phenologies (*A. obscurus*, *G. soricina*, *C. brevicauda*, and *R. pumilio*), whereas three species evinced such geographic variation (*A. lituratus*, *A. planirostris*, and *C. perspicillata*). Climate change will likely alter the seasons and extents of propitious times for reproductive activities, as well as the reliability of proximate cues for initiating reproduction, compromising current reproductive strategies and leading to altered phenological patterns of reproduction or reproductive success, possibly resulting in local extinction of some species.

Key words: bimodal reproductive strategy, breeding season, climate change, frugivores, gleaning animalivores, global change biology, lactation, nectarivores, Phyllostomidae, unimodal reproductive strategy

La selección natural debería favorecer a individuos que sincronicen aspectos de alta demanda de energía en su actividad reproductiva con períodos de alta abundancia y previsibilidad de recursos, lo que conduciría a patrones estacionales de reproducción a nivel poblacional. No obstante, pocos estudios, especialmente estudios sobre murciélagos en el Neotrópico, han utilizado criterios cuantitativos rigurosos para distinguir entre patrones fenológicos ya sea para diferentes poblaciones dentro del mismo hábitat o para la misma especie en diferentes hábitats. Para explorar este tema, cuantificamos los patrones anuales de reproducción de murciélagos machos (porcentaje de la población con testículos escrotales) y hembras (porcentaje de la población embarazada o lactante) en regiones bajas de la Amazonía (alrededores de Iquitos, Perú) a nivel de poblaciones y de ensamblajes. Cinco especies exhibieron patrones unimodales, incluidos *Artibeus obscurus*, *Artibeus planirostris*, *Carollia benkeithi*, *Phyllostomus*

hastatus, y *Rhinophylla pumilio*. Dos especies (*Artibeus lituratus* y *Glossophaga soricina*) mostraron patrones bimodales, con picos reproductivos separados por patrones de inactividad, mientras que cuatro especies (*Carollia brevicauda*, *Carollia perspicillata*, *Sturnira lilium*, y *Sturnira tildae*) mostraron un patrón bimodal en el que los picos de actividad ocurren en tándem, con un primer pico considerablemente más alto que el segundo. Los grupos de frugívoros, animalívoros y nectarívoros exhibieron fenologías reproductivas bimodales, unimodales y bimodales respectivamente. No obstante, la variación interanual en la fenología (es decir, el mes dentro de una temporada en que ocurren los picos en lugar del número de picos por año) caracterizó a cuatro (*A. obscurus*, *C. brevicauda*, *C. perspicillata* y *S. lilium*) de las ocho especies y cada uno de los tres ensamblajes (frugívoros, animalívoros y nectarívoros) con un tamaño de muestra adecuado. Independientemente de la variación en las estrategias, la fenología en la reproducción aumenta la probabilidad de que el parto y el reclutamiento de crías en la población ocurran en la estación húmeda, el período de mayor abundancia de recursos. Cuando comparamos nuestros resultados con los de otras poblaciones de murciélagos mejor estudiadas, cuatro especies no mostraron variación geográfica en sus estrategias reproductivas (*A. obscurus*, *G. soricina*, *C. brevicauda* y *R. pumilio*), mientras que tres especies sí mostraron esta variación geográfica (*A. lituratus*, *A. planirostris* y *C. perspicillata*). Es probable que el cambio climático altere las estaciones y la duración de los periodos propicios para el desarrollo de actividades reproductivas de alta demanda de energía, así como la regularidad de las señales activantes para iniciar la actividad reproductiva, comprometiendo las estrategias reproductivas actuales y conllevando a patrones fenológicos de reproducción alterados, lo que para algunas especies podría resultar en extinciones locales.

Palabras clave: animalívoros, biología del cambio global, cambio climático, estación reproductiva, estrategia reproductiva bimodal, estrategia reproductiva unimodal, frugívoros, lactancia, nectarívoros, Phyllostomidae

From ecological and evolutionary perspectives, reproductive attributes of individuals and populations play critical roles in affecting fitness and local abundance. Natural selection should favor individuals that are able to synchronize energy-demanding aspects of reproductive activity with periods of high resource abundance and predictability (Baker 1938; Bronson 1985). For Neotropical vertebrates in general and for bats in particular, such periods are related to patterns of precipitation because rainfall dynamics affect the timing and abundance of food sources such as fruits, nectar, and insects (Smythe 1986; Marengo et al. 2008).

Most small mammals have evolved a reproductive strategy—live fast and die young—characterized by rapid reproduction in the face of high mortality (Promislow and Harvey 1990). Life history evolution in the Chiroptera has taken a markedly different course, resulting in reproductive strategies for “life in the slow lane” (Barclay and Harder 2003), perhaps as a consequence of their nocturnal and volant habits (Racey and Entwistle 2000). Compared to mammals of similar size, bats are long-lived (Gaisler 1989); have long gestation times with low mass-specific fetal growth rates (Racey 1973; Frazer and Huggett 1974); have small litter sizes, typically one and at most two or three offspring (Racey 1982; Tuttle and Stevenson 1982); produce large offspring (Harvey 1986; Kurta and Kunz 1987); have extended periods of lactation and postnatal care (Hayssen 1993); and reproduce many times during their lifetime (Gaisler 1989). Multiple constraints affect reproductive patterns including short-term energetic costs (Loudon and Racey 1987; Gittleman and Thompson 1988), and longer-term trade-offs associated with compromised body condition and survivorship (Bell 1980; Clutton-Brock et al. 1989). As a consequence of the relatively long life span of bats given their body size, a remarkably diverse suite of reproductive tactics has evolved compared to other orders of mammal (Racey and Entwistle 2000).

Climate change may represent a particularly chronic challenge for species whose life histories reflect life in the slow lane, as they may not be able to evolve with sufficient speed to adapt to changing environmental conditions (Hoffmann and Sgro 2011; Ofori et al. 2017) or recover with dispatch from demographic declines associated with climate-induced disturbance (Isaac 2009).

In general, three basic reproductive strategies characterize phyllostomid bat populations (Family Phyllostomidae; Carter 1970; Fleming et al. 1972; Wilson 1973), which constitute the taxonomic focus of this research given their ease of collection via mist-netting. The strategies include aseasonal polyestry, seasonal polyestry, and seasonal monoestry—each ostensibly related to the phenology of food resources that are consumed by particular species, which are in turn affected by climatic seasonality (Fleming et al. 1972; Wilson 1973; Willig 1985; Molinari and Soriano 2014). Two factors affected by natural selection contribute to population-level patterns of reproduction (e.g., Willig 1985). First, the number of births that an individual can execute successfully in a year is related to its estrous cycle and gestation period (i.e., monoestry represents one birth per year and polyestry represents more than one birth per year). Thus, the nature of individual estrous cycles and length of gestation periods affect the potential modality of reproductive phenologies at the population level. In contrast, the degree of synchrony among individuals within a population determines the realization of particular patterns as seasonal or aseasonal. When estrous cycles are highly synchronized among individuals, seasonal monoestry or polyestry may obtain, whereas asynchronous monoestry or polyestry would lead to the absence of peaks or to the presence of platykurtic peaks.

Early work (Racey 1982; Tuttle and Stevenson 1982) stressed that bat reproduction was labile over time and space, even for individuals of the same species. Nonetheless, only a few

studies (e.g., Taddei 1976; Myers 1977; Willig 1985; Durant et al. 2013; Hazard et al. 2022) have rigorously documented the annual phenologies of Neotropical species, especially in areas of Amazonian rainforest, where local abundance (Castro-Arellano et al. 2007; Willig et al. 2007; Presley et al. 2008), as well as taxonomic (Willig and Selcer 1989; Willig and Sandlin 1991; Stevens and Willig 2002), functional (Stevens et al. 2003), phenetic (Stevens et al. 2006), and phylogenetic (Stevens 2006) biodiversity are greatest for bats.

If climate change continues to affect the seasonal timing and duration of periods of high rainfall and drought, proximate environmental cues may no longer signal the onset of propitious times for reproductive activity or ensure that correspondence of periods of pregnancy and lactation with periods of high resource abundance (Telemeco et al. 2013). Moreover, the evolutionary challenges that consumer organisms face because of climate change may be overwhelming in the short to intermediate term, in part because of dynamics imposed by food-web linkages. Because of their relatively long life spans and low birth rates, it may be particularly challenging for bats (Barclay and Harder 2003), especially those species with small population densities, to rapidly adapt to such changing environmental circumstances. Frugivores and nectarivores must track both climate change and the phenological responses of the plant species that dominate their diets or on the arthropod species for which they obtain supplementary protein during pregnancy and lactation. In addition, bats must be able to adapt to climate-induced phenological changes associated with landscapes that are increasingly dominated by human activities (Presley et al. 2019; Presley and Willig 2022). Moreover, carnivorous bats—including insectivores—must track climatic periods of high rainfall or drought, as well as the phenology of the herbivorous and carnivorous species on which they prey. Given the accelerating speed of climate change (Thompson 2010), it remains to be seen if bat species can adjust reproductive phenologies to accommodate shifts in patterns of precipitation or temperature, and associated resource uncertainties.

Differences in reproductive phenology could be of three general types: those representing contrasting modalities (e.g., continuous, unimodal, bimodal patterns); those reflecting the seasonality of reproductive activity (e.g., peaks in wet season vs. in dry season); or those reflecting the monthly appearance of peaks within seasons. For all types, we expect differences in reproductive phenology among species within a location, as well as among different populations of the same species, as these differences have been empirically documented in the past (e.g., Wilson and Mittermeier 2019) and emerge from considerations of natural selection. Interspecific differences can arise because of species-specific resource requirements that must align with temporal patterns of resource availability, species-specific differences in proximate cues that have evolved to signal the initiation of reproduction, or species-specific life history attributes (e.g., gestation time, estrous cycle) that constrain the number and timing of births per year. Geographic variation in reproductive phenologies within species is expected because

resource composition and productivity—as well as their seasonal patterns—differ among locations, as do the reliability of particular proximate cues, giving rise to different selection pressures on the behavior and physiology of species. Following Durant et al. (2013) and Hazard et al. (2022), we characterize reproductive phenologies of male and female bats for 11 well-sampled species and for three well-sampled ensembles of phyllostomids from lowland Amazonia, make interannual intraspecific, interspecific, and inter-ensemble comparisons within a geographic locality, and relate patterns of reproductive activity to environmental variability associated with seasonality of precipitation (a proxy for productivity).

MATERIALS AND METHODS

Insightful comparisons of reproductive phenologies among species within the same geographic locality, among geographic localities for the same species, or over time for a particular combination of species and geographic locality are predicated on a number of criteria. First, sample sizes per month should be sufficiently large to have confidence that descriptors of monthly reproductive activity (e.g., percent pregnant, percent lactating, percent pregnant and lactating) are accurate reflections of population status. Second, the temporal domain over which data were collected for monthly descriptors of reproductive activity should include all or most months of the year, but should not extend across decades, thereby reducing the effect of long-term environmental variation on descriptors of monthly reproductive activity. Third, the spatial domain over which data were collected should be sufficiently small so as to reduce the effect of larger-scale habitat variation or climatic differences on descriptors of monthly reproductive activity. Fourth, rigorous and consistent criteria should be used to precisely define characteristics that distinguish peaks in reproductive activity over an annual cycle and that distinguish such modality from a uniform pattern.

Research was conducted from September 2001 to December 2005 in association with two large projects concerning the ecology of infectious diseases in lowland Amazonia. One project examined the role of bats as hosts for spirochaete species (*Leptospira* spp.) that cause leptospirosis (Bharti et al. 2003; Matthias et al. 2005), and the other examined the role of bats as reservoir hosts for a variety of arbovirus strains (Weaver and Barrett 2004; Weaver et al. 2004). Within the context of the latter, we were able to institute multiple experimental designs to address ecological questions, including the effects of deforestation resulting from small-scale subsistence farming (Willig et al. 2007, 2019; Presley et al. 2009) and landscape structure (Klingbeil and Willig 2009, 2010) on bat populations and communities. Together, these projects amassed a considerable quantity of information (e.g., over 18,000 capture records), including data on seasonal variation in the reproductive status of bats.

Study area.—The study area was situated in the environs surrounding and south of the City of Iquitos (3.74°S, 73.24°W)

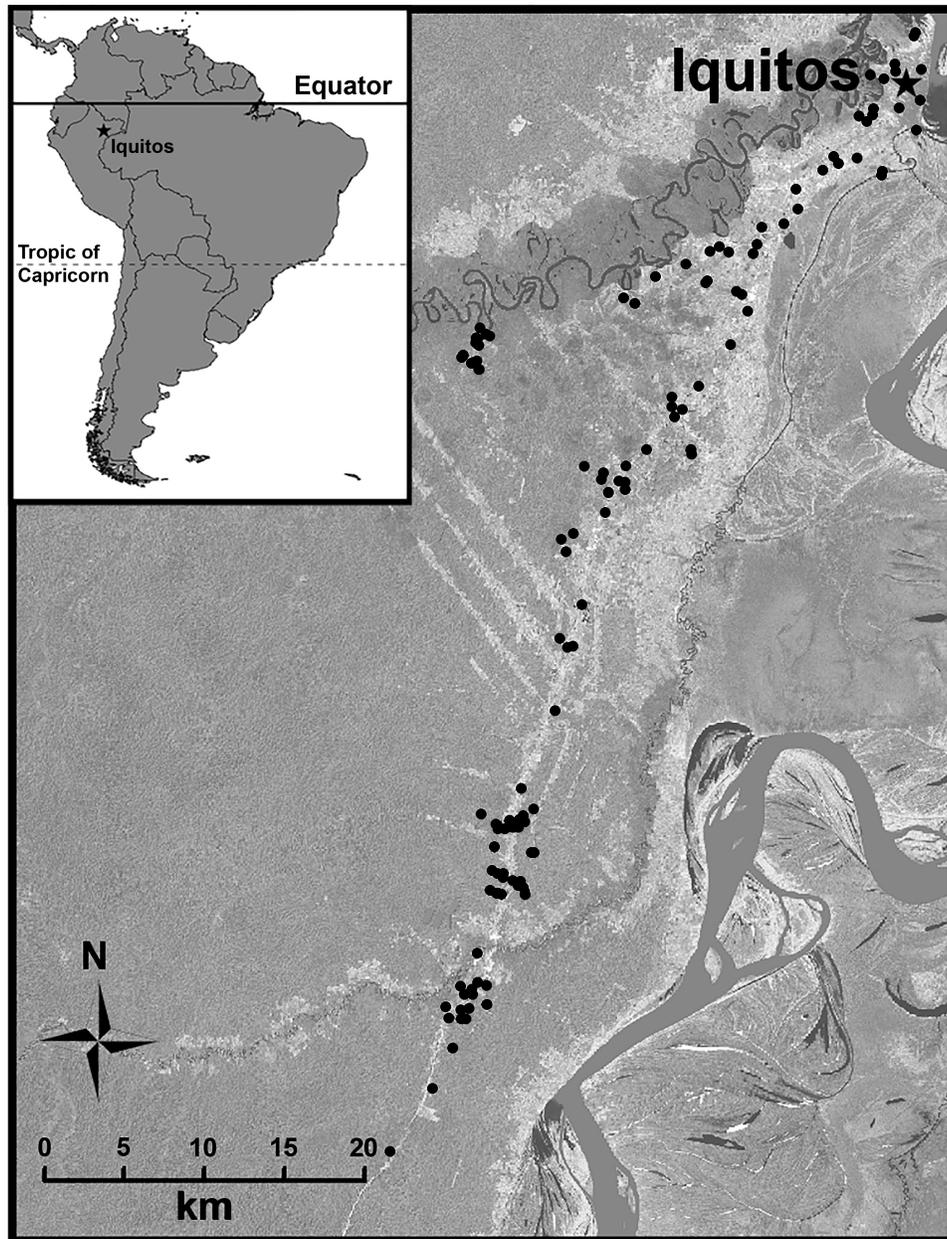


Fig. 1.—Map of the Iquitos region in northwestern Perú, illustrating the extent of deforestation and fragmentation along the Río Itaya and the Iquitos-Nauta Highway. Center of Iquitos is indicated with a star. Survey points at which bats were collected are indicated by black dots. The location of the city of Iquitos, and its relationship to the rest of Perú and South America, appear in the inset.

at the convergence of the Amazon, Nanay, and Ucayali Rivers in the Departamento of Loreto in Perú (Fig. 1). Iquitos is in the Inambari area of endemism (da Silva et al. 2005), which in 2005 had lost <10% of its forest cover and was among the least threatened regions of the Amazon. Based on the Holdridge System (Holdridge et al. 1974), the region is in the Humid Tropical Forest Botanical Province (Tosi 1960). The terrain is rolling, dissected by numerous rivers and streams, and punctuated by low-lying Moriche Palm (*Mauritia flexuosa*) swamps, ponds, and marshes (Vásquez 1997). Elevation ranges from 100 to 220 m ASL, with low-lying areas characterized by flooded forest and higher-elevation areas supporting white sand forest and upland forest.

Anthropogenic activities have produced considerable deforestation along river courses, roadways, and in the vicinity of Iquitos (Nelson et al. 2000); however, less accessible areas remain covered by extensive mature forests (Fig. 1). Deforestation in the region typically occurs at small scales (<3 ha) and results from the establishment of small agricultural fields (locally called ‘chacra’; Mäki et al. 2001). Chacras are planted with pineapple (*Ananas comosus*, Bromeliaceae), plantain (*Musa* spp., Musaceae), or manioc (*Manihot esculenta*, Euphorbiaceae), and are tended until the soil is no longer fertile (~5 to 7 years). The influx of pioneer species into abandoned chacras results in patches of early successional forests (locally

called ‘purma’). Purma differs from mature forest in terms of plant species composition (e.g., *Cecropia* spp. often dominate) and physical structure (<10 m canopy, dense understory). Mature upland forest in the region is characterized by high tree diversity (Vásquez 1997) with a 30-m canopy punctuated by 50-m emergent trees. Chacra and purma typically have clearly defined boundaries and commonly occur adjacent to each other as well as to mature forest.

Climatic regime.—The climate is tropical with an average temperature of 25°C and with precipitation historically ranging from 2,400 to 3,700 mm per year (Marengo 1998). A modest dry season occurs from July to October (Madigosky and Vatnick 2000); however, no time of year is characterized by a water deficit and average monthly rainfall is generally greater than 180 mm for every month. More recent records of precipitation from Iquitos (Weatherspark.com, <https://weatherspark.com/y/24250/Average-Weather-in-Iquitos-Peru-Year-Round#Sections-Precipitation>) corroborate that over the last quarter-century (1996–2020), the dry season experiences a modest reduction in monthly rainfall compared to the wet season, and that considerable variation among half-decade periods (quinquennia) characterizes mean monthly precipitation (Fig. 2). Compared to other quinquennia, the quinquennium (2001–2005) corresponding to this study (Fig. 2) is unremarkable, with each monthly mean occurring within 2 SD of the mean values for all five quinquennia. Nonetheless, mean monthly precipitation during this study was among the most wet of those during the past quarter-century. Interannual variation in precipitation from 2001 to 2005—the time period of bat collection—was considerable, and generally greater for the wet season than for the dry season (Fig. 2). Nonetheless, the amount of monthly precipitation for particular years during the study period was unremarkable (i.e., inside of the 95% confidence interval for the quinquennium).

Bat fauna.—Iquitos harbors a diverse bat community, including 79 species (Table 1) that represent six families and seven guilds (aerial insectivores, frugivores, gleaning animalivores, high-flying insectivores, nectarivores, piscivores, and sanguivores; Wilson 1973). The diversity of functional roles performed and ecosystem services provided by bats makes them important members of tropical rainforests (Lacher et al. 2019). More specifically, Neotropical bats are important agents of pollination and seed dispersal for many species of plants (Fleming and Heithaus 1981; Galindo-González et al. 2000), and their activity promotes secondary succession of disturbed areas (Muscarella and Fleming 2007). Because of their great abundance and ease of capture via mist nets, analyses were restricted to phyllostomids (Supplementary Data SD1), which represent most of the species (55) in the Iquitos region (Willig et al. 2007, 2019; Klingbeil and Willig 2009, 2010).

Bats were surveyed primarily by mist-netting, supplemented by searches of roosts, typically in man-made structures. The number and dispersion of nets per geographic locality, as well as the time periods during which sampling was conducted, were quite variable as a consequence of the different research questions at different times during the

study. In addition, the amount of sampling effort and number of bats captured differed by year due to changing research foci (Supplementary Data SD2). In general, nets remained open from 1800 to 0100 h, were checked every 20 to 30 min, and were closed during heavy rain. Nets were erected at ground level and in the upper understory. Importantly, sampling occurred in a variety of habitat types, including mature, mid-successional, and early successional forests (i.e., purma), as well as agricultural (i.e., chacra), rural, suburban, and urban areas. Often, bats were not marked, and when they were, we could not identify recaptures with confidence if they extended beyond a few months. However, during the two studies within the Arbovirus Project that involved marking individual bats, we did not count recaptured individuals in assessments of reproductive phenology and these studies represented the majority of captures. Additional information

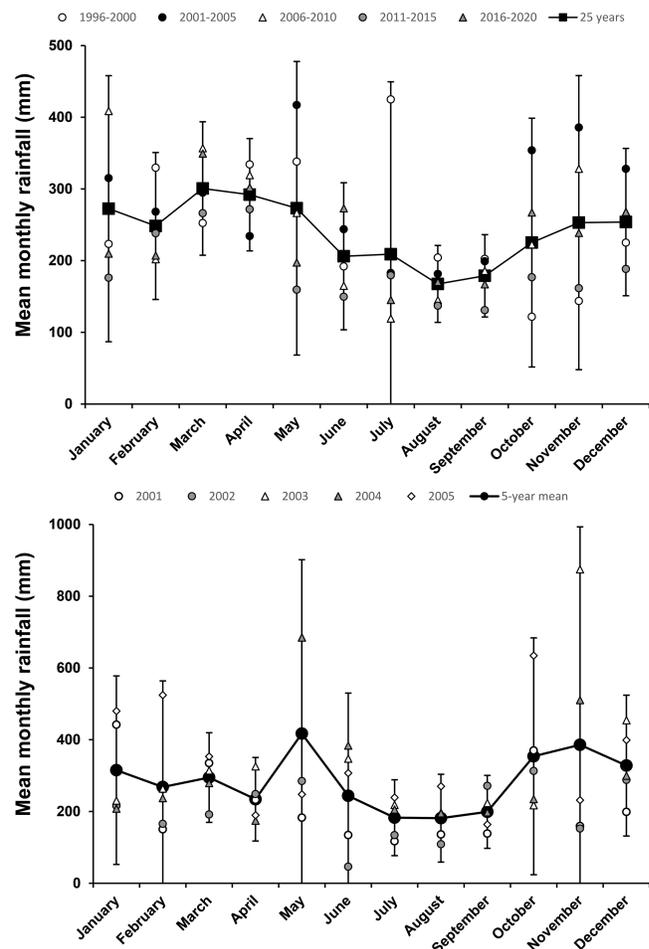


Fig. 2.—Mean monthly rainfall in Iquitos, Perú for each quinquennium from 1996 through 2020 and for that entire quarter-century (upper panel), as well as monthly rainfall for each year during which bats were surveyed in this study (2001–2005) and the mean monthly rainfall for that quinquennium (lower panel). Vertical bars are 95% confidence intervals (± 1.96 SD). Data are from Weatherspark.com (<https://weatherspark.com/y/24250/Average-Weather-in-Iquitos-Peru-Year-Round#Sections-Precipitation>).

Table 1.—List of bat species captured near Iquitos, Perú. Reproductive phenology was analyzed for species in bold.

Family	Family
Subfamily	Subfamily
Species	Species
Emballonuridae	Phyllostomidae
<i>Centronycteris maximiliana</i>	Stenodermatinae
<i>Cormura brevirostris</i>	Artibeus obscurus
<i>Peropteryx leucoptera</i>	Artibeus planirostris
<i>Peropteryx macrotis</i>	<i>Chiroderma salvini</i>
<i>Rhynchonycteris naso</i>	<i>Chiroderma trinitatum</i>
<i>Saccopteryx bilineata</i>	<i>Chiroderma villosum</i>
<i>Saccopteryx leptura</i>	<i>Mesophylla macconnelli</i>
	<i>Platyrrhinus brachycephalus</i>
Phyllostomidae	<i>Platyrrhinus helleri</i>
Desmodontinae	<i>Platyrrhinus infuscus</i>
<i>Desmodus rotundus</i>	<i>Sphaeronycteris toxophyllum</i>
	<i>Sturnira lilium</i>
Glossophaginae	<i>Sturnira magna</i>
<i>Anoura caudifer</i>	<i>Sturnira oporophilum</i>
<i>Choeroniscus minor</i>	<i>Sturnira tildae</i>
<i>Glossophaga soricina</i>	<i>Uroderma bilobatum</i>
<i>Lonchophylla mordax</i>	<i>Uroderma magnirostrum</i>
<i>Lonchophylla thomasi</i>	<i>Vampyressa bidens</i>
	<i>Vampyressa brockii</i>
Phyllostominae	<i>Vampyressa thyone</i>
<i>Chrotopterus auritus</i>	<i>Vampyrodes caraccioli</i>
<i>Glyphonycteris daviesi</i>	
<i>Glyphonycteris sylvestris</i>	Noctilionidae
<i>Lophostoma brasiliense</i>	<i>Noctilio albiventris</i>
<i>Lophostoma carrikeri</i>	<i>Noctilio leporinus</i>
<i>Lophostoma silvicolum</i>	
<i>Micronycteris megalotis</i>	Thyropteridae
<i>Micronycteris minuta</i>	<i>Thyroptera tricolor</i>
<i>Mimon crenulatum</i>	<i>Thyroptera lavalii</i>
<i>Phylloderma stenops</i>	
<i>Phyllostomus discolor</i>	Molossidae
<i>Phyllostomus elongatus</i>	<i>Cynomops planirostris</i>
<i>Phyllostomus hastatus</i>	<i>Eumops bonariensis</i>
<i>Tonatia saurophila</i>	<i>Eumops glaucinus</i>
<i>Trachops cirrhosus</i>	<i>Molossops temminckii</i>
<i>Trinycteris nicefori</i>	<i>Molossops neglectus</i>
<i>Vampyrum spectrum</i>	<i>Molossus rufus</i>
	<i>Molossus molossus</i>
Carollinae	<i>Promops centralis</i>
<i>Carollia benkeithi</i>	
<i>Carollia brevicauda</i>	Vespertilionidae
<i>Carollia perspicillata</i>	<i>Eptesicus brasiliensis</i>
<i>Rhinophylla fischeriae</i>	<i>Eptesicus fernalis</i>
<i>Rhinophylla pumilio</i>	<i>Lasiurus blossevilli</i>
	<i>Lasiurus ega</i>
Stenodermatinae	<i>Myotis albescens</i>
<i>Artibeus anderseni</i>	<i>Myotis nigricans</i>
<i>Artibeus concolor</i>	<i>Myotis oxyotus</i>
<i>Artibeus gnoma</i>	<i>Myotis riparius</i>
<i>Artibeus lituratus</i>	<i>Myotis simus</i>

on the bat fauna and the environs of the study area appears elsewhere (Willig et al. 2007; Klingbeil and Willig 2009, 2010; Presley et al. 2009).

In general, systematic nomenclature follows Simmons (2005), except in recognizing *Carollia benkeithi* (Solari and Baker 2006) rather than *C. castanea*, and considering *Artibeus planirostris* rather than *A. jamaicensis* to occur in Perú (Lim et al. 2004). We classified phyllostomid species into broad foraging guilds (i.e., frugivores, gleaning animalivore, nectarivores, and sanguinivores) based on published

recommendations (Wilson 1973; Gardner 1977), which are consistent with those used in other ecological studies of this fauna (e.g., Klingbeil and Willig 2009, 2010; Willig et al. 2019). Collections of voucher specimens were deposited in the Natural Science Research Laboratory of Texas Tech University in Lubbock, Texas, and in the Museo de Historia Natural of the Universidad Nacional Mayor de San Marcos in Lima, Perú. Research involving live animals followed the guidelines for use of wild mammals in research approved by the American Society of Mammalogists (Sikes et al. 2016), and was approved by the Animal Care and Use Committee of Texas Tech University (ACUC# 01084-03).

Reproductive phenologies.—The reproductive status of individuals was determined via external inspection of live specimens, as well as from examination of individuals that were sacrificed and preserved for taxonomic, ecological, or epidemiological research. Based on visual inspection and palpation of adult females, we classified reproductive status as pregnant, lactating, pregnant and lactating, or inactive. Consequently, we underestimated the proportion of pregnant females because early stages of gestation are difficult to detect without necropsic examination of reproductive tracts. We classified reproductive status of adult males based on visual inspection of testes—males with abdominal testes were considered to be reproductively inactive and males with scrotal testes were considered reproductively active. Regardless of sex, juveniles were distinguished by their smaller size compared to adults, distinctive pelage, and nonossified phalanges.

For each combination of species and sex (species-level analyses) or ensemble and sex (ensemble-level analyses), we summarized reproductive data on a monthly basis, regardless of year. The bases (i.e., denominators) of monthly proportions related to male reproductive activity (percentage of males that possessed scrotal testes) or related to female reproductive activity (i.e., percentage of females that were pregnant, lactating, or pregnant and lactating) were the total number of adults of the corresponding sex that were captured during a particular month. If a specimen was pregnant and lactating, it counted toward the proportion of pregnant and to the proportion of lactating females. Following Hazard et al. (2022), we explored the use of circular statistics (Ruxton 2017; Landler et al. 2018, 2020)—more specifically the Hermans–Rasson test (Landler et al. 2018) and the Rayleigh test (Zar 1999)—to distinguish uniform and nonuniform patterns of reproductive activity. Unfortunately, such tests are not appropriate when the marginal totals (i.e., number of captures per month) arise as a consequence of sampling effort and constrain the number of individuals in any reproductive category during any month. Critically, the demographic response variable is binary (e.g., pregnant vs. not pregnant) and failure to include this inherent categorical characteristic of the response could lead to inaccurate conclusions. Consequently, we did not incorporate such tests into our assessment of reproductive phenologies. Elsewhere, we are developing an approach that combines the output from circular statistical analyses with randomization tests to assess nonrandom deviations from uniformity. This approach is based on the pool of individuals representing each of the binary categories

and constrained to maintain the sample size per month in the simulations to equal the empirical monthly sample size.

For each reproductive characteristic separately, we classified peaks into two categories, primary and secondary (Durant et al. 2013). A primary peak was defined as a period with the highest proportion of reproductive activity bounded by periods with proportions of activity that were less than half the height of the primary peak (the bounds). Secondary peaks were local maxima outside of the temporal range defined by the bounds of the primary peak, but with proportions of reproductive activity that were at least 50% of the height of the primary peak and that were bounded by periods with activities that were less than 50% of the height of the secondary peak or by the boundaries of the primary peak. Importantly, we did not have data on the number of times per year that any particular female was pregnant. Thus, we could not characterize estrous cycles as being monoestrous or polyestrous. Nonetheless, we could characterize population-level patterns based on peaks in reproductive activity.

Interannual variation.—If annual weather patterns and associated phenology of fruiting or flowering—as well as insect emergence and abundance—differ greatly among years, then combining several years of data could obscure annual patterns or lead to inaccuracies, especially biases that could make peaks appear more platykurtic than expected for species that have 4-month periods of gestation (e.g., phyllostomids) or that could obscure multimodal patterns. To address this, we separately evaluated if the monthly proportion of pregnant females was contingent on year for each species of phyllostomid or for each of three foraging ensembles using a three-way (year vs. month vs. reproductive condition) log-linear model (Sokal and Rohlf 1995) in which reproductive condition is the dependent binary variable, and year and month are categorical independent variables (Program Log-linear Logit Analysis, SPSS Version 28.0.0.0). Interannual variation in the monthly pattern of reproductive activity was signaled in cases where the deviations in a model excluding the three-way interaction between reproductive condition, year, and month was significant. If the data are classified into categories representing unique combinations of calendar year and month, the number of such combinations without bats (e.g., 0 pregnant females and 0 nonpregnant females) can strongly affect statistical conclusions, and are relatively frequent at the population level for some species. As a cautionary approach, we considered year to be a contiguous set of 12 months, and perused the data to find an optimal balance between (1) maximizing the number of such annual extents that were compared and (2) minimizing the average number of months in those annual patterns that were represented by 0 captures.

Interspecific and inter-ensemble comparisons.—Two species or ensembles with the same phenological classification (e.g., unimodal) could differ in the monthly details of peaks and troughs in terms of either temporal location (e.g., a mode in August vs. a mode in December) or kurtosis (narrow peak from July to August vs. a broad peak from May to September). To evaluate this, we conducted a three-way (species vs. month

vs. reproductive condition) log-linear model (Sokal and Rohlf 1995) in which reproductive condition is the dependent binary variable and either species and month (interspecific comparisons), or ensemble and month (inter-ensemble comparisons) are categorical independent variables (Program Log-linear Logit Analysis, SPSS Version 28.0.0.0). In all cases, monthly data were combined for all years. Pairwise interspecific comparisons of monthly reproductive phenology or pairwise differences in inter-ensemble comparisons were only undertaken if the corresponding omnibus analysis involving all 11 species or all three ensembles was significant, respectively. Interspecific or inter-ensemble variation in the monthly phenological patterns was signaled in cases where the deviations in a model excluding the three-way interaction between reproductive condition, species, and month or reproductive condition, ensemble, and month, respectively, were significant.

RESULTS

We captured 18,194 bats representing 80 species, 42 genera, and six families (Table 1). Most adult individuals were phyllostomids (16,406), with six genera (Supplementary Data SD1) representing over 90% of phyllostomid bats: *Artibeus* (six species comprising 3,120 individuals); *Carollia* (three species comprising 8,511 individuals); *Glossophaga* (one species comprising 491 individuals); *Phyllostomus* (three species comprising 629 individuals); *Rhinophylla* (two species comprising 1,145 individuals); and *Sturnira* (five species comprising 1,035 individuals). These bats represent four ensembles, which in rank order of abundance were frugivores (32 species comprising 14,428 individuals), gleaning animalivores (16 species comprising 1,215 individuals), nectarivores (six species comprising 700 individuals), and sanguinivores (one species comprising 63 individuals).

To enhance the accuracy of estimated annual patterns of reproduction, we only analyzed data for species or for ensembles if most months (≥ 8) were represented by 10 or more individuals for each sex (Supplementary Data SD1). When fewer than 10 individuals form the basis of a monthly sample, the estimated proportion is subject to considerable uncertainty based on stochastic sampling effects. Using this criterion, we ultimately characterized the annual pattern of reproduction for each of 11 species including five stenodermines—*Artibeus lituratus* (457 adults), *A. obscurus* (725 adults), *A. planirostris* (1,605 adults), *Sturnira lilium* (633 adults), and *S. tildae* (299 adults); one glossophagine—*Glossophaga soricina* (491 adults); four carollines—*C. benkeithi* (541 adults), *C. brevicauda* (2,041 adults), *C. perspicillata* (5,929 adults), and *Rhinophylla pumilio* (1,012 adults); and one phyllostomine—*Phyllostomus hastatus* (393 adults). Similarly, we separately characterized the reproductive patterns of bats in the frugivore (14,428 adults), gleaning animalivore (1,215 adults), and nectarivore (700 adults) ensembles. Captures of sanguinivores (61 adults) were insufficient to support further quantitative analysis at the level of the ensemble.

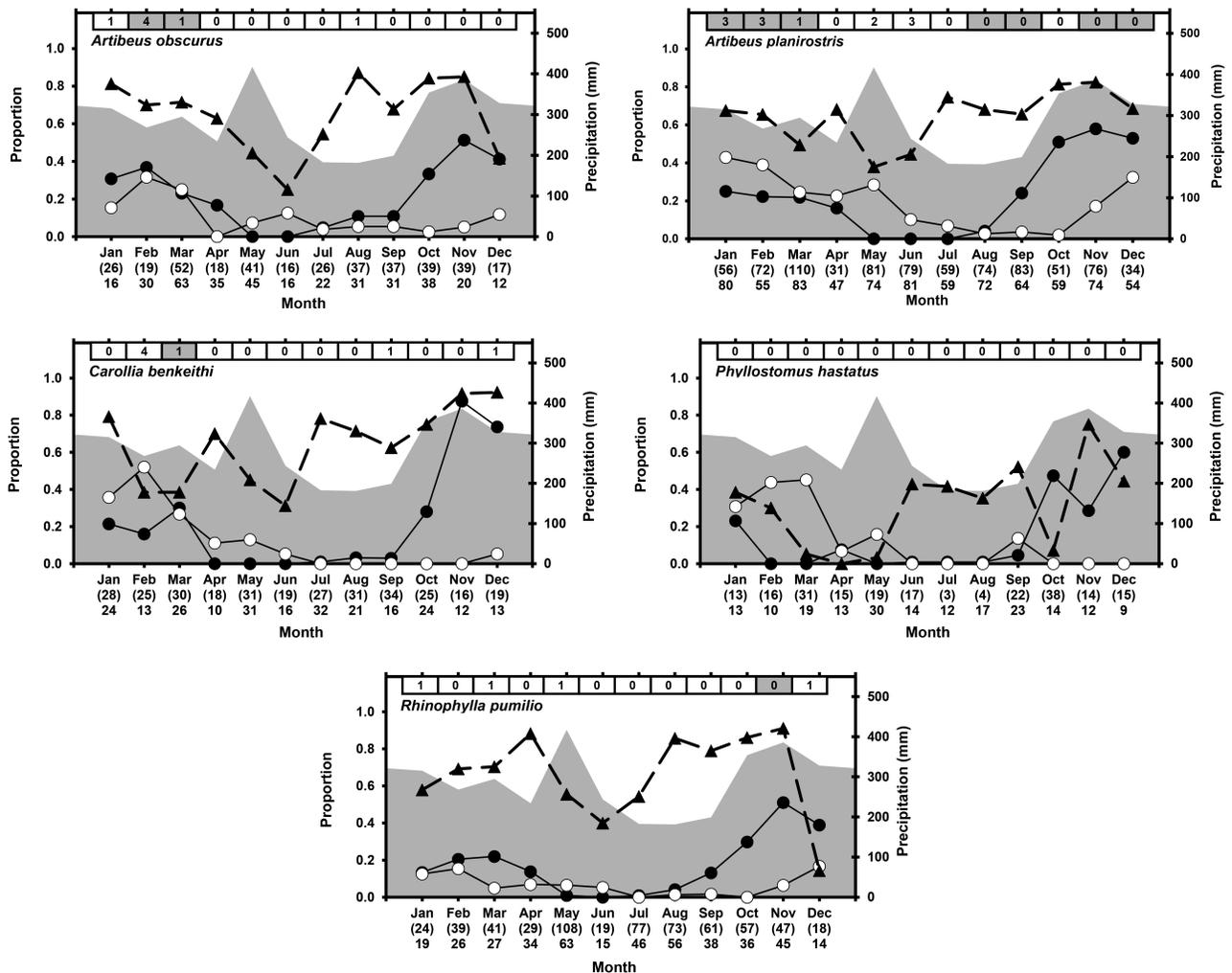


Fig. 3.—Graphical representations of reproductive phenologies of species of bat (*Artibeus obscurus*, *A. planirostris*, *Carollia benkeithi*, *Phyllostomus hastatus*, and *Rhinophylla pumilio*) with unimodal peaks in activity. Shaded background represents mean annual pattern of precipitation for the study area (Iquitos, Perú) for the quinquennium during which bats were captured (see text for details). Filled circles represent proportions of adult females that were pregnant. Open circles represent proportions of adult females that were lactating. Total numbers of adult females (bases for previous proportions) are indicated by parenthetical numbers below each month. Filled triangles represent proportions of adult males with scrotal testes. Total numbers of adult males (bases for previous proportions) are indicated by numbers below each month that are not in parentheses. Numbers in the horizontal row above each graph represent the number of captured juveniles; shaded boxes in that row represent months during which some adult females were simultaneously pregnant and lactating.

To categorize reproductive phenology, we primarily used monthly patterns of pregnancy augmented by monthly patterns of lactation for females, although we documented monthly patterns of testis condition for males as well. We classified five species as exhibiting unimodal phenologies (Fig. 3), two species as exhibiting bimodal phenologies with reproductive peaks separated by periods of inactivity (Fig. 4), and four species as exhibiting bimodal phenologies in which peaks in activity occur in tandem without an intervening period of inactivity (Fig. 5).

Population-level reproductive phenologies

Unimodal patterns.—In the environs of Iquitos, unimodal patterns of reproduction are generally indicated by a cycle in which (1) the proportion of pregnant females is greatest late

in the year (September through December) and then decreases early the following year, (2) the proportion of lactating females follows a similar pattern to pregnancy with about a 2-month time lag compared to the pattern of pregnancy, and (3) a single and protracted period occurs from April through August during which few pregnant or lactating females occur in the population (Fig. 3). Overall, the initiation of reproductive activity (pregnancy) occurs toward the beginning (July for *A. obscurus*), in the middle (August for *A. planirostris*, *C. benkeithi*, *R. pumilio*), or toward the end (September for *P. hastatus*) of the dry season, increasing the likelihood that the time of lactation and recruitment of independently foraging young into the population corresponds to the period of greatest resource abundance, which typically occurs during the wet season (Smythe 1986; Marengo et al. 2008).

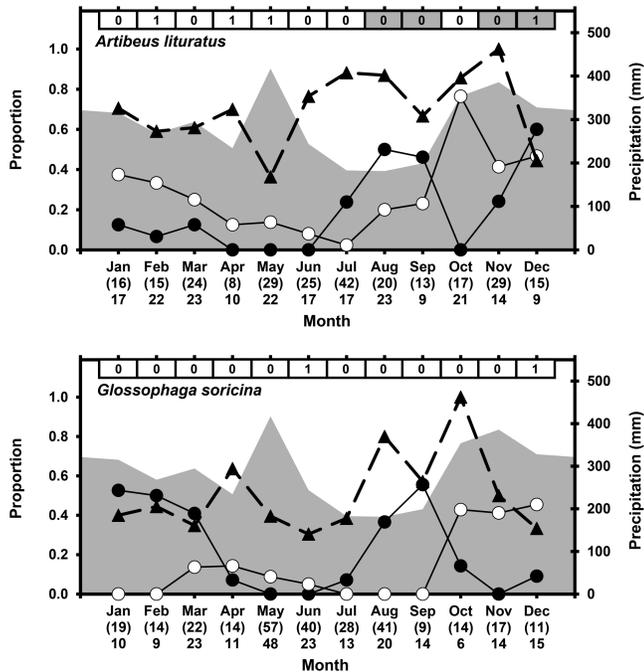


Fig. 4.—Graphical representations of reproductive phenologies of species of bat (*Artibeus lituratus* and *Glossophaga soricina*) with bimodal peaks in activity separated by a period of nonpregnancy. Shaded background represents mean annual pattern of precipitation for the study area (Iquitos, Perú) for the quinquennium during which bats were captured (see text for details). Filled circles represent proportions of adult females that were pregnant. Open circles represent proportions of adult females that were lactating. Total numbers of adult females (bases for previous proportions) are indicated by parenthetical numbers below each month. Filled triangles represent proportions of adult males with scrotal testes. Total numbers of adult males (bases for previous proportions) are indicated by numbers below each month that are not in parentheses. Numbers in the horizontal row above each graph represent the number of captured juveniles; shaded boxes in that row represent months during which some adult females were simultaneously pregnant and lactating.

1: *Artibeus obscurus*.—Females of this frugivorous species are pregnant from July to April, with a peak of 51% pregnant in November (Fig. 3). Lactation occurs in all months except April and peaks in February. Juvenile individuals appear in the population from January to March, but also in August. Males with scrotal testes are common in each month of the year.

2: *Artibeus planirostris*.—Females of this frugivorous species are pregnant from August until April, with a peak of 50–58% pregnant from October to December (Fig. 3). In contrast, lactation occurs year-round, but only exceeds 10% of captured females from November until June. The number of pregnant or lactating females is at its lowest from June through August. Juvenile individuals appear in the population from January to June. Males with scrotal testes are common in each month of the year.

3: *Carollia benkeithi*.—Females of this species of frugivore are pregnant from August to March, with a large peak of about 92% pregnant in November (Fig. 3). Lactation occurs from

December to June with a peak in February. A broad period of little to no reproductive activity (<10% pregnant or lactating) spans June to September. Juvenile individuals appear in the population from September to March. Males with scrotal testes are common throughout the year, but with a broad peak from July to January.

4: *Phyllostomus hastatus*.—Females of this species of gleaning animalivore are pregnant from September until April, with a peak of 60% pregnant from October to December (Fig. 3). Lactation peaks from January to March. The number of pregnant or lactating females is at its lowest from June through August (<10% pregnant or lactating). Juvenile individuals were never captured during the study period. Males with scrotal testes are common from June to February and absent or rare from March to May.

5: *Rhinophylla pumilio*.—Females of this species of frugivore are pregnant from August to May, with a peak of 51% pregnant in November (Fig. 3). Lactation occurs during most months, generally at low levels (<10%), and peaks from December to February. A broad period of little to no reproductive activity (<10% pregnant or lactating) spans May to August. Juvenile individuals appear in the population from December to May. Males with scrotal testes are common throughout the year. Although this species exhibits a unimodal reproductive pattern in the environs of Iquitos based on a priori criteria, some evidence suggests a bimodal pattern with a secondary peak in March, but the proportion of pregnant females during the second peak and the separation between peaks are not sufficiently large to result in a bimodal classification.

Bimodal patterns.—In general, two kinds of bimodal patterns characterized reproductive phenologies of bats in the Amazon. In the first pattern (i.e., *A. lituratus* and *G. soricina*), each of two modal cycles was followed by a period of reproductive inactivity (Fig. 4). Thus, two seasons of reproductive activity as well as two periods of reproductive inactivity occur per year. In the second pattern (i.e., *C. brevicauda*, *C. perspicillata*, *S. lilium*, and *S. tildae*), periods of reproductive activity are in tandem, and sometimes indistinct from each other (Fig. 5), with the primary peak often markedly higher than the secondary peak and no clear period of inactivity between the peaks. Thus, one extended period of reproductive activity with two peaks, and one variably long period of inactivity occur per year. Regardless of these differences, the initiation of reproductive activity (pregnancy) occurs toward the beginning (July for *A. lituratus*, *C. brevicauda*, *G. soricina*, *S. tildae*, *S. lilium*) or in the middle (August for *C. perspicillata*) of the dry season, increasing the likelihood that the time of greatest recruitment of independently foraging young into the population corresponds to the period of greatest resource abundance, which typically occurs during the wet season (Smythe 1986; Marengo et al. 2008).

1: *Artibeus lituratus*.—Females of this species of frugivore are pregnant from July to March, with a primary peak of 60% pregnant in December, and a secondary peak of about 45–50% pregnant from August to September (Fig. 4). The absence of any pregnant females in October reinforces the bimodal

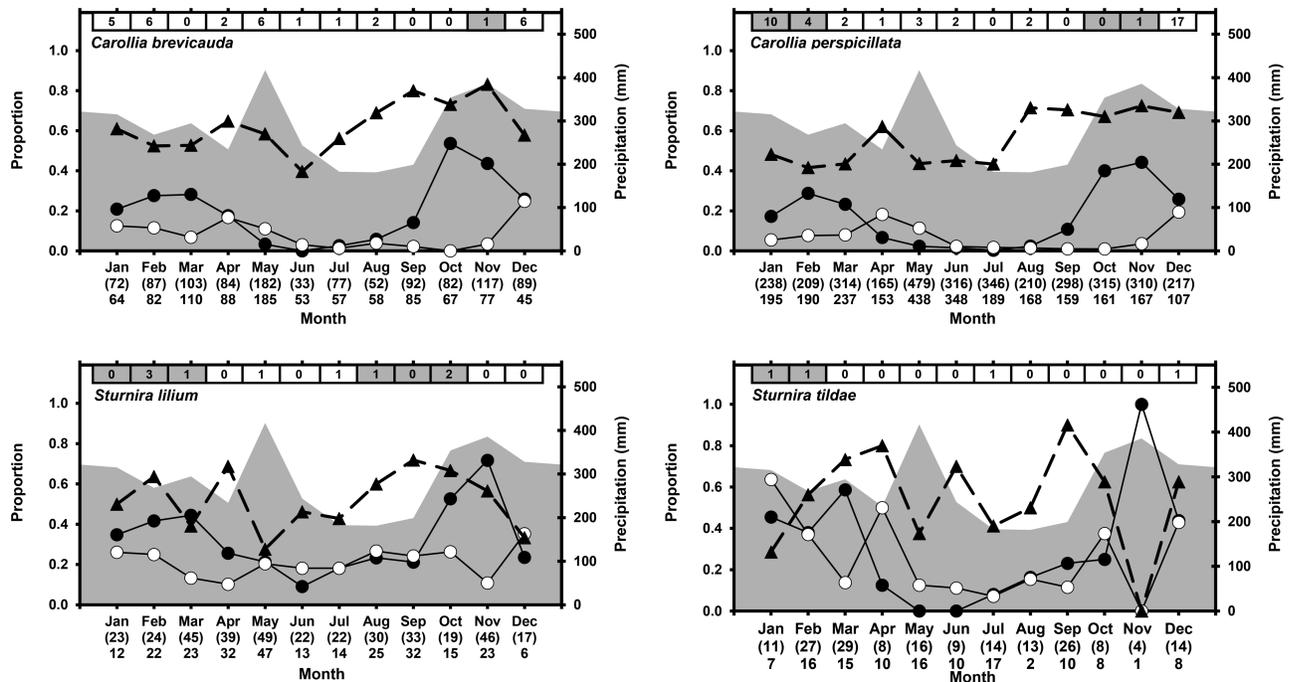


Fig. 5.—Graphical representations of reproductive phenologies of species of bat (*Carollia breviceauda*, *Carollia perspicillata*, *Sturnira lilium*, and *S. tildae*) with bimodal peaks in activity that overlap and occur in tandem (not separated by periods of nonpregnancy). Shaded background represents mean annual pattern of precipitation for the study area (Iquitos, Perú) for the quinquennium during which bats were captured (see text for details). Filled circles represent proportions of adult females that were pregnant. Open circles represent proportions of adult females that were lactating. Total numbers of adult females (bases for previous proportions) are indicated by parenthetical numbers below each month. Filled triangles represent proportions of adult males with scrotal testes. Total numbers of adult males (bases for previous proportions) are indicated by numbers below each month that are not in parentheses. Numbers in the horizontal row above each graph represent the number of captured juveniles; shaded boxes in that row represent months during which some adult females were simultaneously pregnant and lactating.

reproductive pattern. Lactation begins in August, peaks in October, and continues until June. Juvenile individuals appear in the population from December to May. Males with scrotal testes are common from throughout all months.

2: *Glossophaga soricina*.—Females of this species of nectarivore are pregnant in all months except May, June, and November, with a large peak of 57% pregnant in September, and a similarly large peak of 52% pregnant from January to February (Fig. 4). Lactation also evinces two peaks—a primary one from October to December, and a much smaller one from March to April. The absence of any pregnant females in November, and the absence of any lactating females from January to February reinforces a bimodal reproductive pattern. Juvenile individuals were only captured in June and September. Males with scrotal testes are common in each month of the year.

3: *Carollia breviceauda*.—Females of this species of frugivore are pregnant in all months except June, with a primary peak of 54% pregnant from October to November and a secondary peak of 28% pregnant from February to March (Fig. 5). Lactation occurs in all months except October, with a primary peak in December and a secondary peak in April. A broad period of little to no reproductive activity (<10% pregnant or lactating) spans June to August. Juvenile individuals were captured in all months except for March, September, and October.

Males with scrotal testes are common in each month of the year.

4: *Carollia perspicillata*.—Females of this species of frugivore are pregnant in all months, with a large peak of 40–45% pregnant from October to November and a smaller peak of 29% pregnant from February to March (Fig. 5). Lactation occurs during all months, generally at low levels (<10%), with peaks in December and in April. A broad period of low reproductive activity (<10% pregnant or lactating) spans June to August. Juvenile individuals were captured in all months except for July, September, and October. Males with scrotal testes are common during all months.

5: *Sturnira lilium*.—Females of this species of frugivore are pregnant throughout the year, with a primary peak of 72% pregnant from October to November and a secondary peak of about 44% pregnant from February to March (Fig. 5). Lactation occurs during each month at low to modest levels (10–20%), but with a primary peak in December and a broad secondary peak from August to October. Juvenile individuals were captured idiosyncratically throughout the year in February, March, May, July, August, and October. Males with scrotal testes are common in each month of the year.

6: *Sturnira tildae*.—Females of this species of frugivore are pregnant in all months except May and June, with a primary peak of 100% pregnant in November (sample size was low,

$n = 4$) and a secondary peak of 58% pregnant in March (Fig. 5). Lactation occurs during all months, except for November (sample size was low, $n = 4$), with a primary peak in January and secondary peak in April. Juvenile individuals were captured from December to February as well as in July. Males with scrotal testes are common throughout the year, except during November (sample size was low, $n = 1$). Although this species exhibits a bimodal reproductive pattern in the environs of Iquitos, the certainty of this is lessened because of the small sample size in November that could have inflated estimates of pregnancy due to chance alone (i.e., four pregnant females in a sample size of 4 is not particularly strong evidence for the primary peak).

Ensemble-level reproductive phenologies

The reproductive phenology of each ensemble is a composite of contributions from many taxa (32 species of frugivore, 15 species of gleaning animalivore, and six species of nectarivore). Nonetheless, ensemble-level patterns are dominated by the contributions of the more abundant species discussed in the population-level section.

Frugivore ensemble.—Females are pregnant during all months, with a primary peak of 47% pregnant in November and a secondary peak of 29% pregnant in February (Fig. 6). This arises because abundant frugivores with unimodal phenologies (five species) have a single peak of pregnancy in November (four species) or December (one species), and those with a bimodal phenology (five species) have a primary peak in October (one species), November (three species), or December (one species), as well as a secondary peak in August (one species), February (one species), or March (three species). Lactation occurs during all months, and peaks in December. Juvenile individuals are present in all months, and attain highest abundance from December through February. Males with scrotal testes are common in each month of the year. In general, the initiation of reproductive activity occurs in the earlier portions of the dry season (July and August), increasing the likelihood that the time of recruitment of independently foraging young into the population corresponds to the period of greatest resource abundance, typically the wet season.

Gleaning animalivore ensemble.—Females are pregnant in all months, with a broad peak of 40–48% pregnant that spans October through December (Fig. 6). Lactation occurs during all months, except July, and peaks in February. Juvenile individuals are present during 6 months and attain their greatest abundance in June. Males with scrotal testes are common in each month of the year. In general, the initiation of reproductive activity occurs between the end of the wet season and beginning of the dry season, increasing the likelihood that the time of recruitment of independently foraging young into the population corresponds to the period of greatest resource abundance.

Nectarivore ensemble.—Females are pregnant during all months, except for May and November, with two equivalent peaks in pregnancy (Fig. 6), one in September (53% pregnant) and one in February (50% pregnant). Lactation occurs from October through June, and peaks in December. Juveniles

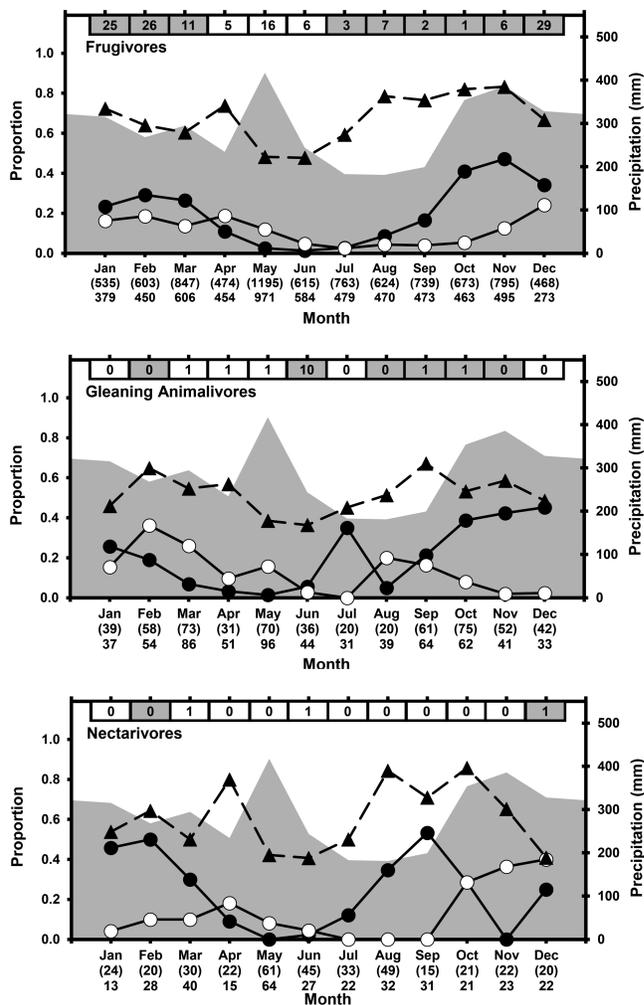


Fig. 6.—Graphical representations of reproductive phenologies of three phyllostomid ensembles: frugivores, gleaning animalivores, and nectarivores. Shaded background represents mean annual pattern of precipitation for the study area (Iquitos, Perú) for the quinquennium during which bats were captured (see text for details). Filled circles represent proportions of adult females that were pregnant. Open circles represent proportions of adult females that were lactating. Total numbers of adult females (bases for previous proportions) are indicated by parenthetical numbers below each month. Filled triangles represent proportions of adult males with scrotal testes. Total numbers of adult males (bases for previous proportions) are indicated by numbers below each month that are not in parentheses. Numbers in the horizontal row above each graph represent the number of captured juveniles; shaded boxes in that row represent months during which some adult females were simultaneously pregnant and lactating.

were captured rarely. Males with scrotal testes are common throughout the year. This ensemble-level pattern mostly parallels the phenology of the most abundant nectarivore, *G. soricina* (Fig. 6). The initiation of reproductive activity occurs between the end of the wet season and beginning of the dry season, increasing the likelihood that the time of recruitment of independently foraging young into the population corresponds to the period of greatest resource abundance, typically the wet season.

Temporal variation in reproductive phenologies

Analyses of temporal variation in reproductive phenology were not conducted for *A. lituratus*, *P. hastatus*, and *S. tildae* because of the prevalence of months with no captures of female bats. For the other species, analyses were based on 36 continuous months of data, either May 2002 to April 2005 (*A. obscurus*, *C. perspicillata*, *G. soricina*, *R. pumilio*, and *S. lilium*) or June 2002 to May 2005 (*A. planirostris*, *C. benkeithi*, and *C. brevicauda*), or 24 continuous months of data (May 2022 to April 2004 for *G. soricina*). Analyses for ensembles were based on 36 continuous months of data, May 2002 to April 2005 (frugivores and nectarivores) or June 2002 to May 2005 (gleaning animalivores). In general, significant temporal effects on reproductive phenology were related to interannual differences in the timing of peaks within seasons, rather than to changes in modality or to changes in the season of reproductive activity (Supplementary Data SD3).

Population level.—The role of interannual variability on the reproductive phenologies of female bats differed among species based on consideration of patterns of pregnancy (Table 2). Significant interannual variability characterized four species of bat (*A. obscurus*, *C. brevicauda*, *C. perspicillata*, and *S. lilium*)—but in contrast, did not characterize the reproductive phenologies for four other species (*A. planirostris*, *C. benkeithi*, *G. soricina*, and *R. pumilio*). Nonsignificance generally occurred when the number of captured female bats within the multiyear data set was relatively small (i.e., *G. soricina*, 207 individuals) or when species exhibited a unimodal reproductive phenology (i.e., *A. planirostris*, *C. benkeithi*, *R. pumilio*). Importantly, even these “small” sample sizes are large compared to those

used in most studies of Neotropical bat reproductive phenology (Supplementary Data SD4).

Ensemble level.—Interannual variability characterized the reproductive phenologies based on consideration of patterns of pregnancy for each ensemble (Table 2). The degree of significance increases with increasing sample size.

Interspecific or inter-ensemble variation in reproductive phenologies

Interspecific (three-way logit analysis—likelihood ratio test, statistic = 384.9, d.f. = 110, $P < 0.001$ and Pearson's χ^2 test, statistic = 405.6, d.f. = 110, $P < 0.001$) and inter-ensemble (three-way logit analysis—likelihood ratio test, statistic = 135.1, d.f. = 22, $P < 0.001$ and Pearson's χ^2 test, statistic = 174.9, d.f. = 22, $P < 0.001$) differences in reproductive phenology were significant in omnibus analyses. Interspecific differences in monthly reproductive phenology were common, and significant in about 65% of the 55 possible comparisons (Fig. 7). Moreover, many of those significant pairwise interspecific differences reflected inter-ensemble comparisons (i.e., in 95% of the 20 possible interspecific comparisons involving different ensembles). The nectarivore (*G. soricina*) was significantly different from all other species (i.e., nine frugivores and one foliage gleaner). In addition, the foliage gleaner (*P. hastatus*) was significantly different from all species, except for *A. planirostris* (i.e., eight frugivores and one nectarivore). The extent of pairwise interspecific difference in the monthly reproductive phenology between all possible pairs of the nine frugivores was quite variable and significant in slightly over half of the 36 possible comparisons—*A. lituratus* (eight interspecific differences), *S. lilium*

Table 2.—The extent to which monthly reproductive phenologies (log odds ratio of pregnant to nonpregnant individuals) differ among annual extents (consecutive 12-month periods) for each of seven species of frugivore, one species of nectarivore, and three ensembles was evaluated by a log-linear analysis (logit model) with reproductive state (pregnant vs. not pregnant) as the dependent binary variable and annual extent and month (January through December) as categorical independent variables. The two separate tests of the significance (likelihood ratio and Pearson's χ^2) generally result in similar levels of significance, enhancing the confidence in any conclusion about interannual variation in monthly reproductive phenologies. Analyses were not conducted for *Artibeus lituratus*, *Phyllostomus hastatus*, or *Sturnira tildae* because of the prevalence of months in which no individuals were captured. Significant results are bold.

Ensemble Species	Number of individuals	Likelihood ratio		Pearson's χ^2	
		Value	P-value	Value	P-value
Species-level analyses					
Frugivores					
<i>A. lituratus</i>	Insufficient monthly data				
<i>A. obscurus</i>	352	38.82	0.015	37.59	0.020
<i>A. planirostris</i>	757	18.13	0.698	20.17	0.572
<i>C. benkeithi</i>	299	20.41	0.558	18.67	0.666
<i>C. brevicauda</i>	1,007	44.09	0.003	42.44	0.006
<i>C. perspicillata</i>	3,246	87.15	<0.001	79.63	<0.001
<i>R. pumilio</i>	562	23.79	0.358	21.63	0.482
<i>S. lilium</i>	329	52.79	<0.001	51.14	<0.001
<i>S. tildae</i>		Insufficient monthly data			
Gleaning animalivores					
<i>P. hastatus</i>		Insufficient monthly data			
Nectarivores					
<i>G. soricina</i>	207	12.85	0.303	13.00	0.293
Ensemble-level analyses					
Frugivores	7,784	158.15	<0.001	164.94	<0.001
Gleaning Animalivores	580	42.31	0.006	41.87	0.006
Nectarivores	338	36.57	0.026	33.58	0.054

et al. 1975; Lobo et al. 2003). This variation in flowering phenology results in variation in fruit phenology, which likely also explains the tendency for some frugivores and the frugivore ensemble to exhibit bimodal reproductive phenologies. In contrast to bats with plant-based diets, gleaning animalivores exhibit a unimodal reproductive phenology with an extended peak (Fig. 6), likely reflecting the prolonged high resource availability represented by the great diversity of invertebrates during the wet season (Racey 1982; Nurul-Ain et al. 2017).

Whereas differences between ensembles in reproductive phenology are related to differences in the phenologies of the resource bases they rely on (primarily nectar, fruit, insects), differences between frugivores in reproductive phenologies likely represent subtle differences between species of bat in the fruit that they preferentially consume (i.e., that differ in fruiting phenology), which reflect either the effects of competition (Fleming 1986; Bonaccorso and Gush 1987) or the ghost of competition past (Connell 1980). The need to reduce competitive effects via differences in reproductive phenology may be important during multiple stages of reproduction to ensure sufficient resources during pregnancy and lactation, as well as to increase the likelihood of survival of newly fledged juveniles.

Intraspecific comparison among geographic localities.—The application of similar quantitative criteria to those used herein for categorizing the reproductive phenologies facilitates intraspecific comparisons from lowland Amazonia of Peru with populations from Caatingas habitats of Brazil (Willig 1985), edaphic Cerrado habitats of Brazil (Willig 1985), Caribbean lowlands of Costa Rica (Durant et al. 2013), and Central Amazonia of Brazil (Hazard et al. 2022). The general reproductive phenologies of populations (unimodal vs. bimodal) did not differ among geographic localities for four species: *A. obscurus* (unimodal in lowland Amazonia and Central Amazonia); *G. soricina* (bimodal in lowland Amazonia, Caribbean Highlands, Caatingas, and edaphic Cerrado); *C. brevicauda* (bimodal in lowland Amazonia and Central Amazonia); and *R. pumilio* (unimodal in lowland Amazonia and Central Amazonia). These interpopulational similarities suggest strong phylogenetic constraints at the level of species or similarities in temporal patterns of production among sites. In contrast, three species evinced geographic variation in reproductive phenologies: *A. lituratus* (bimodal in lowland Amazonia and edaphic Cerrado, but unimodal in Central Amazonia); *A. planirostris* (unimodal in lowland Amazonia but bimodal in Caatinga and edaphic Cerrado); and *C. perspicillata* (bimodal in lowland Amazonia, Caatinga, and edaphic Cerrado, but unimodal in Central Amazonia). These interpopulational differences suggest that phylogenetic constraints are weak at the level of species or large differences in temporal patterns of production among sites.

Many other studies provide insights into geographic variation in the reproductive activity and phenology of phyllostomid bats (Supplementary Data SD4). Nonetheless, comparison of our results with most of those studies is fraught with issues related to quantitative approaches, small sample sizes, and a lack of data to characterize reproductive activities for a complete annual cycle. Many such studies represent serendipitous opportunities to note reproductive activity without suitable data

to characterize reproductive phenologies. Consequently, it is typically not possible to synthesize incomplete information from various localities to characterize geographical variation in reproductive phenologies for most species of Neotropical bats. Nonetheless, some notable patterns emerge. For example, populations of *A. lituratus* (Duarte and Talamoni 2010) or *S. lilium* (Mares and Wilson 1971) from more seasonal habitats (e.g., Atlantic Rainforest, eastern Paraguay, Argentina) have shorter breeding seasons, with one peak in activity, compared to the extended bimodal activity observed in populations from northern South America, Central America, Mexico, or Amazonia (Fig. 4; Wilson and Mittermeier 2019). In contrast, *G. soricina* and *C. perspicillata* consistently exhibit bimodal reproductive patterns throughout much of their range in Mexico (Ramirez-Pulido et al. 1993), Brazilian Cerrado (Zortea 2003), and Amazonia (Fig. 4) for *G. soricina*; Costa Rica (Fleming et al. 1972), Panama (Fleming 1988), Brazilian Atlantic Forest (Fazzolari-Correa 1995), French Guiana (Cosson and Pascal 1994), and Amazonia (Fig. 4) for *C. perspicillata*—with the timing of reproduction determined by the flowering phenology of the local plant communities.

Future prospects.—The nature of population-level phenologies is affected by a number of factors including those reflecting the environment and those related to the biology of particular species. Environmental factors include seasonality of critical resources (i.e., energy- or nutrient-rich food), duration of periods with elevated levels of such critical resources, magnitude of stress associated with periods of reduced critical resources, and existence of accurate indicators of favorable or unfavorable circumstances (Clarke 1981; Racey 1982; Heideman 2000). Biological factors include length of gestation period, length of period during which offspring are dependent on mothers for nourishment via lactation, and capacity of females to undergo multiple estrous cycles (Carter 1970; Racey 1982; Harvey 1986). Based on first principles, if the propitious period is short compared to time associated with gestation or lactation, interindividual synchrony should be elevated with single birth peaks that are leptokurtic (narrow and steep). In these cases, the risk of a substantial fitness cost for failing to match reproduction with resource production during the propitious period is high because of the likely reduced body condition of females—affecting survivorship of offspring—and failure of females to successfully give birth or wean offspring, or recruit independently foraging young of the year into the population (Racey 1982). In contrast, if the propitious period is long compared to the time associated with gestation or lactation, then interindividual synchrony could be low, with one of two outcomes. When the propitious period cannot accommodate two contiguous periods of gestation, then a single platykurtic peak (broad and shallow) may characterize reproductive activity. Alternatively, if the propitious period can accommodate two or more contiguous periods of gestation, then multiple leptokurtic peaks may characterize reproductive activity. Moreover, reduced synchrony or eurykurtic peaks would be enhanced if environmental cues are not accurate predictors of future propitious periods (i.e., bet hedging may be a successful strategy). Synchrony or leptokurtic peaks would be expected if the cost

of improperly timing reproductive activity is high (i.e., reduced fitness associated with failed pregnancy or juvenile death), or environmental predictors are not accurate.

Reproductive phenologies documented from early in the 21st century serve as useful comparators to evaluate the ongoing effects of climate change in the Amazon. Due to increases in the frequency of El Niño and La Niña weather patterns, Amazonian rainforests are experiencing more frequent and severe drought conditions and floods (Anderson et al. 2018; Bodmer et al. 2018). Drought in particular can affect timing and success of reproduction in Neotropical bats, as water deficit reduces the available resources (e.g., nectar, fruit, insects) necessary for successful recruitment (Adams 2010). Over the past two decades, the Amazon has experienced three severe droughts, one of which affected the Iquitos region. As drought can severely impact flowering and fruit production, severe drought can potentially cause mass mortality events for frugivorous and nectarivorous bats, and even moderate droughts could reduce successful reproduction (Frick et al. 2019), which requires about 4 months for gestation and about 2 months until weaning (Barclay and Harder 2003). Analyses of interannual variation in reproductive phenologies (Table 2) show that some species exhibit behavioral plasticity and can adjust the timing of reproduction to the particular conditions that occur each year. As climate change may result in alterations in the seasonality of critical resources or in the correspondence between future productivity and the environmental cues used by bats to initiate reproductive activity, maintenance of populations may be challenging for this slowly reproducing taxon (Barclay and Harder 2003). Environmental shifts that exceed the capacity of bat populations to adjust their reproductive strategies will result in demographic declines, increasing the risk of local extinction with detrimental effects on biodiversity and ecosystem processes (Brodie et al. 2014; Kehoe et al. 2021). This may be particularly problematic in Neotropical forests that rely on bats for pollination and seed dispersal, which enhance forest biodiversity and the rate of succession after disturbances (Muscarella and Fleming 2007). Nonetheless, some research is emerging that life history characteristics can evolve relatively rapidly to maintain lifetime reproductive success (Mundinger et al. 2022). Future research should focus on life history characteristics related to reproductive success in bats, with renewed efforts to provide baseline data on reproductive phenology of species against which response to global change can be evaluated quantitatively.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Number of adult female and male bats captured each month for species and guilds whose reproductive phenologies were evaluated.

Supplementary Data SD2.—The total number of adult female, adult male, and juvenile bats captured during each year.

Supplementary Data SD3.—For each of 11 species of bat as well as for each of three guilds, the number of pregnant females captured each month of each year and the percent of captured females that were pregnant each month of each year.

Supplementary Data SD4.—Intraspecific comparisons of reproductive phenologies among studies.

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