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ORIGINAL ARTICLE

Reproductive phenologies of phyllostomid bats in the Central Amazon

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Abstract

Mammals tend to align their most energetically demanding phenological events with periods of peak resource availability. Their reproductive phenology is influenced by local resource availability, potentially leading to geographical variation in their breeding strategy. Although the Amazon is the world's epicenter of bat diversity, the reproductive phenology of Amazonian bats remains poorly known. Seasonality induces fluctuations in resource availability and most phyllostomid species, crucial agents of seed dispersal, pollination and arthropod suppression in the Neotropics, have been described to exhibit seasonal bimodal polyestry. However, current understanding of phyllostomid reproductive phenology is impaired by the paucity of comparative examinations of the phenologies of sympatric species, using consistent classification schemes based on the number and timing of annual peaks in pregnancy and lactation. Using a multi-year dataset from Central Amazonia, we examined the reproductive phenology of nine bat species (*Artibeus concolor, A. obscurus, A. lituratus, Carollia brevicauda, C. perspicillata, Gardnerycteris crenulatum, Lophostoma silvicolum, Rhinophylla pumilio,* and *Trachops cirrhosus*), as well as two feeding ensembles (i.e., frugivores and gleaning animalivores). Only three of the nine species exhibited a bimodal reproductive phenology. Six species and the frugivore ensemble showed unimodal reproductive phenology, while gleaning animalivores displayed an amodal pregnancy pattern. All species except *L. silvicolum* had their primary pregnancy peak during the mid-dry season. A reproductive peak during the early wet season, or local variation in the duration of the fruiting season may explain the deviation of our observations from the expected bimodal polyestry.

Keywords Chiroptera · Neotropical bats · Phyllostomidae · Reproduction · Seasonality

Introduction

Phenology, the study of recurrent biological life cycle events, is key for understanding how organisms react to seasonal changes in dynamic environments (Stucky et al. 2018). As most organisms time their reproduction to

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capitalize on optimal resource abundance, phenology is vital for understanding how population-level dynamics are modulated by environmental cues (Rocha et al. 2017a). This is particularly important in the context of human-induced global change, as phenomena such as climate and land-use change are shifting the timing of vital phenological events (Hällfors et al. 2020).

Reproduction is one of the most energetically demanding aspects of an animal's life cycle (Harshman and Zera 2007). The energy budget of small mammals is heavily constrained by the maintenance costs of physiological parameters associated with the regulation of body temperature, body functioning and foraging (Bronson 1985; McNab 1982; Speakman and Thomas 2003). As most small mammals are unable to store large amounts of energy in the form of fat (Bronson 1985), the energetic demands associated with reproduction are therefore counterbalanced by reproducing seasonally, and at times that are likely to increase reproductive success by allowing for increased food intake (Bronson 1985; Kunz et al. 1995). Additionally, during pregnancy and lactation, bats spend most of their flight time foraging (Kurta et al. 1989). This increased flight activity is energetically extremely costly (Thomas 1975), leading to a tight association between most species' reproductive phenology and periods of high resource availability (Racey and Speakman 1987; Kurta et al. 1989; Racey and Entwistle 2000). For female bats, reproductive costs are mostly shared between pregnancy and lactation for which the daily costs can be twice as high as the costs of pregnancy (Kurta et al.1989; Kunz et al. 1995). As female bats need to increase their food intake to be able to meet these energetic demands (Kunz et al. 1995), food availability is an important determinant of the timing of reproduction (Thompson 1992).

Throughout the tropics, seasonality is mostly shaped by differences in precipitation and not so much by fluctuations in temperature (MacArthur 1984). Seasonal changes in precipitation affect plant and animal phenology, causing oscillations in resource availability (Bentos et al. 2008; Ramos Pereira et al. 2010), one of the main factors controlling the parturition period in bats (Arlettaz et al. 2001). If births were to mismatch peaks of food availability, bat fitness would be negatively affected (Ransome 1989). Weaning, a period during which juvenile bats have to overcome the double challenge of meeting the energetic demands for growth while learning how to independently forage, is critical for juvenile survival (Handley et al. 1991). Thus, in the tropics, female bats seem to avoid giving birth too close to the dry season so that weaning can occur when resources are plentiful, maximizing the survival chances of the offspring (Willig 1985). Accordingly, bat reproduction has been observed to match periods of high resource abundance (Nurul-Ain et al. 2017; Molinari and Soriano 2014; Mello et al. 2004; Estrada and Coates-Estrada 2001; Fleming et al. 1972).

Phyllostomids are one of the most species-rich and ecologically diverse tropical bat families (Fleming 2020; Yoh et al. 2020). The ca. 200 recognized species have evolved to explore a wide range of food sources, ranging from fruits, nectar and pollen, to arthropods, small vertebrates and blood (Fleming et al. 2020). In the Neotropics, food resources such as insects and fruits are available year-round, but their abundance tends to increase during the rainy season and with the onset of rains (da Silva et al. 2011; Torres and Madi-Ravazzi 2006; Ramos Pereira et al. 2010). Across the Neotropics, phyllostomids seem to have adapted to these constraints by adopting a phenology known as *bimodal polyestry*, consisting of the production of two young between the end of the dry season and the middle of the wet season (Wilson 1973; Ribeiro de Mello and Fernandez 2000; Willig 1985; but see, e.g., Duarte and Talamoni 2010 for exceptions to bimodal polyestry). However, plant phenology, and vertebrate and invertebrate prey dynamics vary across forest types and locations (Patricia and Morellato 2011; Hällfors et al 2020), with some Neotropical biomes displaying seasonal fruiting patterns with fruiting peaks occurring during the wet season (Malizia 2001; Alencar et al. 1979; Peres 1994), while others show aseasonal (Alencar 1990; Wallace and Painter 2002) or bimodal patterns with both peaks occurring during the dry season (ter Steege and Persaud 1991). Notwithstanding the scarcity of assemblage-wide phenology studies in Neotropical bats, this variation in resource availability seems to greatly influence bat phenology throughout the region (Estrada and Coates-Estrada 2001; Bernard 2002; Durant et al 2013; de Carvalho et al 2019).

Here, we address the information gap in tropical bat phenology by describing the reproductive phenology of nine Central Amazonian phyllostomid species, as well as two feeding ensembles, frugivores and gleaning animalivores. We compare our results to findings from other locations across the Neotropics in order to identify and explore the underlying drivers of geographic variation in phenology across species' ranges. We anticipated that the reproductive activity of most species will be modulated by seasonality, likely reflecting the timing of maximum fruit and arthropod availability.

Materials and methods

Study site and climate

This study was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP), a whole-ecosystem experimental manipulation located ca. 80 km north of Manaus in the Central Brazilian Amazon (2° 20′ S, 60° 6′ W, 30–125 m.a.s.l.; Fig. 1). The BDFFP was established in the 1980s to assess the effects of forest fragment size

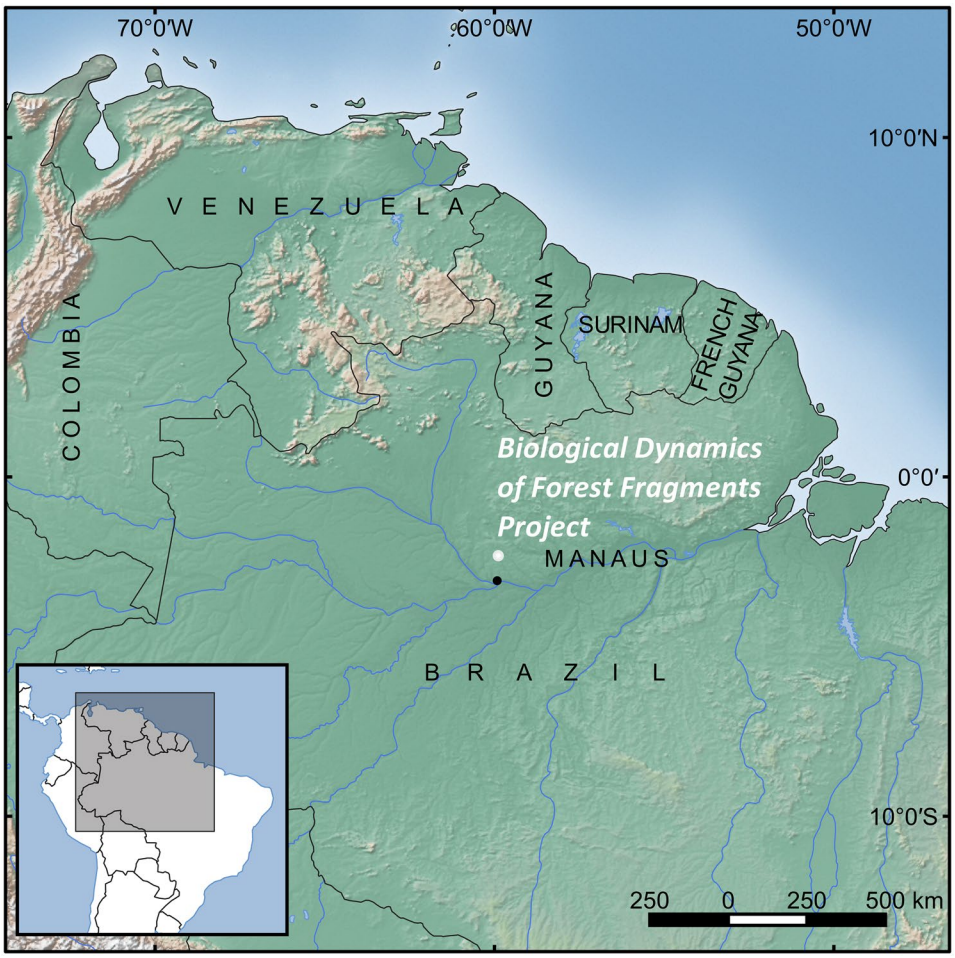

Fig. 1 Location of the Biological Dynamics of Forest Fragments Project (BDFFP), Central Amazon, Brazil

on tropical ecosystems (Lovejoy and Bierregaard 1990). To do so, forest fragments (1, 10, and 100 ha) were isolated from nearby continuous *terra firme* rainforest by distances of 80–650 m. Forest fragments were originally located within cattle ranches but became gradually surrounded by secondary forest dominated mainly by *Vismia* spp. and *Cecropia* spp. (Carreiras et al. 2014; Rocha et al. 2018). Primary forest reaches 30–37 m in mean canopy height, with isolated trees up to 55 m tall (Laurance et al. 2011). Rainfall varies from 1900 to 3500 mm annually, with a dry season between July and November and a rainy season between November and June (Ferreira et al. 2017). Precipitation can exceed 300 mm/month in the wet season, while being under 100 mm/month during the dry season (Laurance et al. 2011; Fig. 2). The flowering peak occurs during the transition between the wet and the dry season, and the fruiting peak occurs at the beginning of the wet season (Haugaasen and Peres 2005, 2007; Bentos et al. 2008).

Bat surveys

Bats were surveyed between August 2011 and October 2014, using both ground- and canopy-level mist nets placed in a variety of habitats: continuous primary forest, forest fragments and secondary forest in which standardized surveys were conducted, as well as temporary lakes, rivers, streams, and clearings where we sampled opportunistically (Farneda et al. 2015; Silva et al. 2020; Rocha et al. 2020; Torrent et al. 2018). Sampling started at dusk and mist nets were deployed until 0:00 a.m., being revised at intervals of ~ 20 min. Captured bats were identified to species level using available field guides and morphological keys (López-Baucells et al. 2018) and standard morphometric (e.g., forearm length and body mass) and demographic data were collected following Handley et al. (1991). The extent of ossification of the phalanges was used to distinguish between adults and juveniles. Pregnant females were identified through gentle palpation of the abdomen and lactating females were identified according

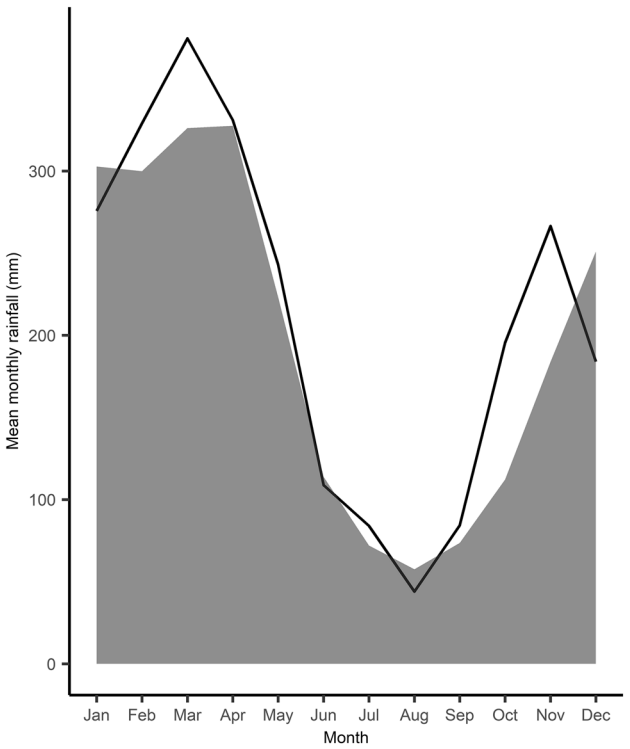

Fig. 2 Average monthly precipitation during the study period (2011–2014, solid line) relative to the long-term average (1991–2020, shaded area). Pluviometry and temperature data was obtained from http://climexp.knmi.nl, associated with the Tropical Rainfall Measuring Mission (TRMM). Data for the period 2011–2014 is based on a satellite-driven monthly precipitation index centred on Manaus at − 3.10 N, −60.00 E, 60 m altitude

to the condition of the mamma (i.e., milk, evidence of hair loss around the nipples). Since small fetuses may go undetected through palpation, the number of nonreproductive adult females may be an overestimate. Bat capture and handling was conducted following guidelines approved by the American Society of Mammalogists (Sikes and Gannon 2011). Taxonomy follows López-Baucells et al. (2018) except for *Mimon crenulatum* which is referred to as *Gardnerycteris crenulatum* (Hurtado et al. 2014). Detailed site descriptions and sampling methods can be found in Rocha et al. (2017b), Silva et al. (2020), Rocha et al. (2020), and Torrent et al. (2018).

Classification of reproductive phenologies

We classified population- and ensemble-level reproductive phenologies following Durant et al. (2013). For adult female bats, we counted the number of pregnancy and lactation peaks. In accordance with Durant et al. (2013), we considered two types of peaks: a *primary peak*, defined as the period with the higher proportion of pregnant/lactating females, bounded by periods where the proportion of pregnant/lactating females was at least twice as low; and *secondary peak*(s), defined in a similar manner but with the difference that the proportion of the secondary peaks was at least 50% of the proportion of the primary peak. Depending on the number of peaks along the year, we expected to observe four different phenological patterns: *amodal* if there was no peak in reproduction/lactation but nonreproductive females were detected throughout the year; *unimodal* if there was one peak in reproduction followed by a peak in lactation; *bimodal* if there were two peaks in reproduction, each followed by peaks in lactation; and *polymodal* if there were more than two peaks in reproduction. Due to the lack of recapture data we were not able to identify if a given individual female was pregnant more than once a year. As such, similarly to Durant et al. (2013), we were unable to classify species according to the five traditional reproductive phenologies (aseasonal monoestry, aseasonal polyestry, seasonal monoestry, seasonal bimodal polyestry and seasonal polyestry; Wilson 1973). Notwithstanding the lack of data regarding the number of estrous cycles (monoestrous [single] vs polyestrous [multiple]) for our study populations, whenever possible we use available literature from elsewhere to discuss the recorded type of estrous cycle of our target species.

According to the seasonal variation of our study area, we defined six periods: June–July, August–September and October–November, respectively as the early, mid and late dry season, and December–January, February–March and April–May, respectively as the early, mid and late dry seasons. At the species and ensemble level, a species/ensemble was retained in the analysis if at least five adult females were captured in a minimum of four periods. At the species level, nine species met these requirements, six of which are frugivores and three are gleaning animalivores (Table 1). These conditions were also met by two ensembles: frugivores and gleaning animalivores. The species included in ensemble level analysis were those listed in Table 1 in addition to *Ametrida centurio, Artibeus cinereus, Artibeus gnomus, Mesophylla macconnelli, Sturnira tildae* and *Vampyressa bidens* for the frugivores, and *Tonatia saurophila* for the gleaning animalivores.

Data analysis

For data analysis, the proportion of pregnant, lactating, and nonreproductive female bats for each species/ensemble was calculated as the number of individuals falling into each category, divided by the total number of females captured for that species/ensemble. At the ensemble level, the proportion of bats falling in each category was weighted by species-specific bi-monthly abundance.

We used circular statistics to test the deviation of the number of pregnant and lactating females throughout the

Table 1 Summary of tests for departure from uniformity based on the Hermans–Rasson and Rayleigh test, respectively, for pregnant adult female bats

Species	Ensemble	Hermans–Rasson test				Rayleigh's test			Graphical analysis		
		Captures	*T*	*p*	Distribution	*z*	*p*	Distribution	Phenology	Primary peak	Secondary peak
Artibeus concolor	F	24	717.66	> 0.001	Non uniform	0.592	> 0.001	Non-uniform	Bimodal	Mid/late dry	Late wet
Artibeus lituratus	F	8	27.31	> 0.001	Non uniform	1	0	Non-uniform	Unimodal	Mid dry	–
Artibeus obscurus	F	15	966.59	> 0.001	Non uniform	0.359	0.145	Uniform	Unimodal	Mid dry	–
Carollia brevicauda	F	9	229.90	> 0.001	Non uniform	0.982	0	Non-uniform	Bimodal	Mid dry	Late wet
Carollia perspicillata	F	315	17,835.71	> 0.001	Non uniform	0.622	0	Non-uniform	Unimodal	Mid dry	–
Gardnerycteris crenulatum	GA	8	452.77	0.032	Non uniform	0.269	0.577	Uniform	Unimodal	Mid wet	–
Lophostoma silvicolum	GA	15	1,561.21	0.075	Uniform	0.508	0.018	Non-uniform	Polymodal	Mid dry	Late dry
Rhinophylla pumilio	F	62	3,432.89	> 0.001	Non uniform	0.326	0.001	Non-uniform	Unimodal	Mid dry	–
Trachops cirrhosus	GA	14	1,280.02	0.004	Non uniform	0.339	0.203	Uniform	Bimodal	Mid dry	Late wet
	Frugivores	450	27,172.47	> 0.001	Non uniform	0.550	0	Non-uniform	Unimodal	Mid dry	–
	Gleaning animalivores	23	4,455.97	> 0.001	Non uniform	0.171	0.240	Uniform	Amodal	–	–

Ensemble abbreviations: *F* Frugivorous bats, *GA* Gleaning animalivorous bats. The season in which the primary and secondary peaks occur was indicated only when it was relevant to the amodal, unimodal or bimodal character of the reproductive phenology, and indicated by "–" if it was not relevant

year from uniformity at the species and ensemble level. The use of circular statistics to test for temporal differences in the number of pregnant and lactating females is justified by the inherent periodicity of pregnancy and lactation data (Landler et al. 2018; Ruxton 2017). An improved version of the Hermans–Rasson test presented in Landler et al. (2019) as well as the Rayleigh test (Zar, 1999) were performed in order to test for departure from a uniform distribution. These tests have similar purposes, but they were both performed because contrary to other classical circular tests like the Rayleigh test or the Watson's *U* test, the Hermans-Rasson test is robust to data with a bimodal distribution (Landler et al. 2019). However, the robustness of the improved version of the Hermans–Rasson test has not been assessed yet (Landler et al. 2019). The Rayleigh test, which is robust to highly grouped data, was therefore also performed (Humphreys and Ruxton 2017). Both tests were implemented using the package *circular* (Jammalamadaka and Sengupta 2001) and the code provided by Landler et al. (2019). Graphics were made with the package *ggplot2* (Wickham 2016) in the software R (Core R Team 2019), and rose diagrams were made in the software Oriana (Kovach 2013).

Results

Nine phyllostomids met the minimum capture numbers established for the phenology analyses and classification at the species level. This included six frugivorous bats (*Artibeus concolor, A. obscurus, A. lituratus, Carollia brevicauda, C. perspicillata,* and *Rhinophylla pumilio*) as well as three gleaning animalivores (*Lophostoma silvicolum*, *Gardnerycteris crenulatum,* and *Trachops cirrhosus*).

Notwithstanding some minor discrepancies, the results of the Hermans–Rasson (H–R) and Rayleigh (R) tests were largely consistent. For pregnancy, both tests suggested that *A. concolor, A. lituratus, C. brevicauda, C. perspicillata, R. pumilio,* and the frugivore ensemble exhibited non-uniform distributions, meaning that they display at least one peak in pregnancy (Table 1). However, non-uniform pregnancy distributions were suggested for *A. obscurus, G. crenulatum, T. cirrhosus,* and gleaning animalivorous bats by the H-R test, but not by the R test. On the other hand, *L. silvicolum* was identified as having a uniform distribution based on the H–R test but a uniform distribution with the R test. For lactation, both tests suggested that *A. lituratus, C. perspicillata, L. silvicolum, R. pumilio*, as well as the frugivore and gleaning animalivore ensembles exhibited non-uniform distributions, meaning that they display at least one peak in lactation (Table 2). However, the results of the H–R and R tests were contradictory for *T. cirrhosus* (uniform lactation according to H–R but non-uniform according to R) and to *A. concolor* and *C. brevicauda* (non-uniform lactation according to H-R but uniform according to

Table 2 Summary of the different analyses for the lactating adult female bats

Species	Ensemble	Hermans–Rasson test				Rayleigh's test			Graphical analysis		
		Captures	T	p	Distribution	z	p	Distribution	Phenology	Primary peak	Secondary peak
Artibeus concolor	F	8	545.34	0.006	Non uniform	0.184	0.775	Uniform	Uni- or bimodal	?	?
Artibeus lituratus	F	22	1,287.69	> 0.001	Non uniform	0.403	0.026	Non uniform	Uni- or bimodal	?	?
Artibeus obscurus	F	3	–	–	–	–	–	–	Unimodal	Mid wet	–
Carollia brevicauda	F	11	1,193.76	0.037	Non uniform	0.180	0.710	Uniform	Bimodal	Mid dry	Mid wet
Carollia perspicillata	F	172	18,081.98	> 0.001	Non uniform	0.166	0.009	Non uniform	Uni- or bimodal	?	?
Gardnerycteris crenulatum	GA	4	–	–	–	–	–	–	Unimodal	Late dry	–
Lophostoma silvicolum	GA	9	195.10	> 0.001	Non uniform	0.570	0.049	Non uniform	Unimodal	Mid dry	–
Rhinophylla pumilio	F	35	3,114.86	> 0.001	Non uniform	0.379	0.006	Non uniform	Unimodal	Late dry	–
Trachops cirrhosus	GA	9	808.81	0.122	Uniform	0.717	0.006	Non uniform	Bimodal	Early dry	Late dry
	Frugivores	263	28,599.91	> 0.001	Non uniform	0.141	0.003	Non uniform	Bimodal	Mid wet	Late dry
	Gleaning animalivores	13	2,343.58	> 0.001	Non uniform	0.418	0.006	Non uniform	Unimodal	Late dry	–

Ensemble abbreviations: *F* Frugivorous bats, *GA* Gleaning animalivorous bats. For the graphical analysis, unclear patterns were marked as '?'. Calculations were not performed when sample sizes were < 5 (indicated as "–"). The season in which the primary and secondary peaks occur was indicated only when it was relevant to the amodal, unimodal or bimodal character of the reproductive phenology, and indicated by "–" if it was not relevant

R). Five out of the nine species, namely *A. lituratus*, *A. obscurus*, *C. perspicillata*, *G. crenulatum,* and *R. pumilio* exhibited a unimodal pregnancy distribution, and so did the frugivore ensemble, even when the more common species *C. perspicillata* was excluded (Figs. 3, 4 Supplementary Fig. 1). However, pregnancy was bimodal for *A. concolor, C. brevicauda,* and *T. cirrhosus,* amodal for gleaning animalivorous bats and, according to Durant et al. (2013)'s definition, the pattern for *L. silvicolum* was polymodal (Table 1, Figs. 3, 4 Supplementary Fig. 1). With the exception of *L. silvicolum,* all species and feeding ensembles display their primary pregnancy peak during the mid-dry season, indicating a high degree of interspecific pregnancy synchronization (Figs. 3, 4 Supplementary Fig. 1). Likewise, other than *L. silvicolum,* all species displaying a secondary pregnancy peak experienced it during the late wet season (Table 1).

As for lactation, *A. obscurus, G. crenulatum, L. silvicolum, R. pumilio,* and the gleaning animalivores ensemble exhibited a unimodal distribution, whereas *A. concolor, A. lituratus, C. brevicauda, C. perspicillata, T. cirrhosus,* and the frugivore ensemble displayed a pattern in accordance with a bimodal distribution (including when *C. perspicillata* was excluded) (Figs. 3, 4). However, due to the lack of information for the early wet season, it is unclear whether the lactation pattern of *A. concolor, A. lituratus,* and *C. perspicillata* was unimodal or bimodal. The primary lactation peak occurred during the mid–wet season for *A. obscurus* and the frugivore ensemble, during the mid–dry season for *C. brevicauda* and *L. silvicolum,* during the late dry season for *G. crenulatum, R. pumilio,* and the gleaning animalivores, and during the early dry season for *T. cirrhosus*, indicating a lower degree of interspecific lactation synchronization (Table 2). Except for *C. brevicauda*, all species displaying a bimodal lactation phenology had their secondary lactation peak during the late dry season.

At the ensemble level, frugivores and gleaning animalivores exhibited distinct reproductive patterns. In the case of frugivores, pregnancies were concentrated in the mid dry season, while for gleaning animalivores, high levels of pregnancy were observed throughout the year, with a peak occurring during the mid-wet season. Regarding lactation, while a bimodal phenology with a primary peak during the mid-wet season and a secondary peak during the late dry season was observed for frugivorous species, a bimodal pattern with a primary peak during the late dry season was observed for gleaning animalivores.

Discussion

Despite the importance of studies on reproductive phenology to better understand the energetic requirements of species over time, assessments using rigorous classification

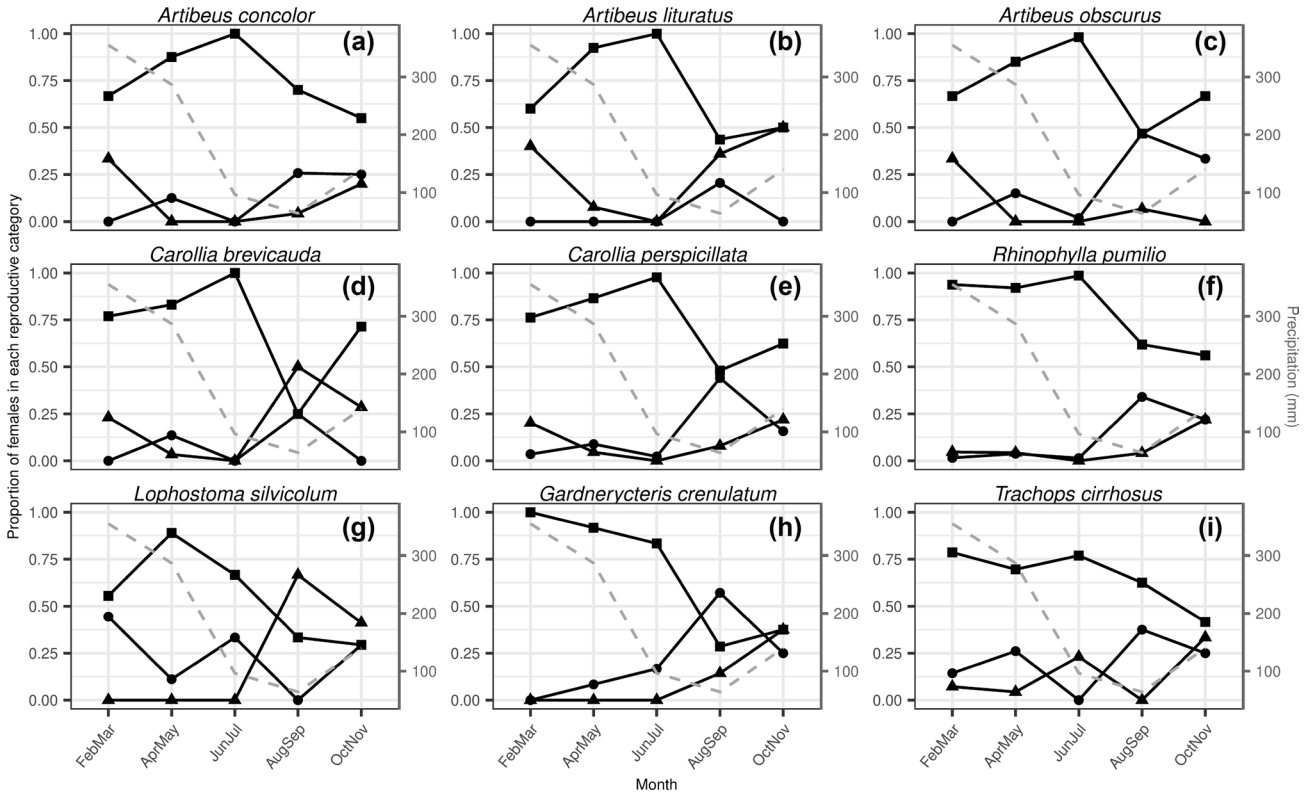

Fig. 3 Reproductive phenology of the nine phyllostomid species considered for species level analysis, based on the proportion of reproductive (lactating and pregnant) females for each species. Dashed grey lines show the average monthly precipitation between 2011 and 2014 at the BDFFP. Black circles represent the monthly proportion of adult pregnant females, black triangles represent the monthly proportion of adult lactating females, and black squares represent the monthly proportion of non-reproductive adult females

approaches for tropical bat species are scarce. Here, we described the phenology of nine of the most common Amazonian phyllostomids, providing the first consistent analysis of reproductive phenology for four out of nine species studied. Our results indicate that most species exhibit a high degree of synchronization of their pregnancy and lactation peaks. This adds to an expanding body of evidence suggesting that the reproductive phenology of Neotropical bats is largely modulated by seasonality and its associated shifts in resource availability (Hernández-Aguilar and Santos-Moreno 2020; Lima and Fabián 2016).

Although over 160 bat species occur throughout the Amazon (López-Baucells et al. 2018), very little is known about the reproductive phenology of most of these species. Indeed, with the exception of a few isolated observations of pregnant or lactating individuals of *Artibeus concolor* (Bernard 2002), *A. obscurus* (Bernard 2002; Albuja 1999), *Gardnerycteris crenulatum* (Pedro et al. 1994; Mello and Pol 2006), and *Rhinophylla pumilio* (Rinehart and Kunz 2006; Bernard 2002; Rocha et al. 2017a), no comprehensive study has been conducted to specifically assess the reproductive phenology of these species.

In the Neotropics, a common pattern is that frugivorous phyllostomids generally experience a reproductive peak during the late dry season and a second peak during the mid-wet season (Fleming et al. 1972; Molinari and Soriano 2014; Durant et al. 2013). In some species, this trend is often facilitated by the ability of bats to delay the development of the embryo and produce milk while pregnant, a phenomenon known as postpartum oestrus, enabling them to give birth twice a year (Ortega et al. 2021). Yet, while all but one of the focal species showed a primary pregnancy peak during the mid-dry season, only two of the six species considered—*A. concolor* and *Carollia brevicauda*—exhibited gestation patterns characteristic of bimodal phenology. *Carollia brevicauda* was observed to be bimodally polyestrous in the Venezuelan Andes (Molinari and Soriano 2014) and Costa Rica (La Val and Fitch 1977). However, Torres et al. (2018) found that *C. brevicauda* reproduces throughout the year with very low synchrony in Colombia. Additionally, at the BDFFP, *A. lituratus*, *A. obscurus,* and *C. perspicillata* evinced a unimodal gestation phenology, suggesting some divergence from previous findings. The reported number of reproductive peaks varies geographically for these species

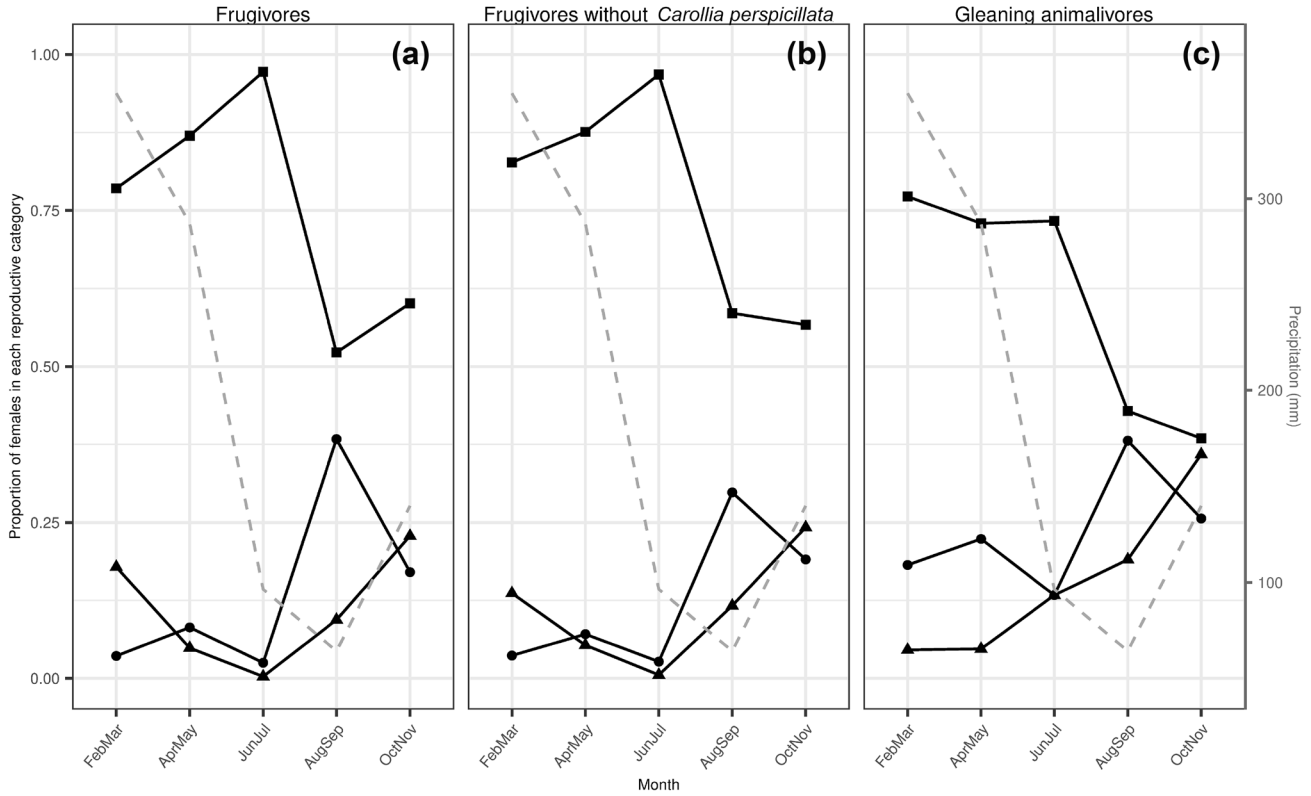

Fig. 4 Reproductive phenology of frugivorous and gleaning animalivorous phyllostomids between 2011 and 2014, determined using the proportion of reproductive (lactating and pregnant) females for each ensemble. Black circles represent the monthly proportion of adult pregnant females, black triangles represent the monthly proportion of adult lactating females, and black squares represent the monthly proportion of non-reproductive adult females

and, corroborating our results, Duarte and Talamoni (2010) reported *A. lituratus* as a seasonally monoestrous species in Brazil. Yet, Fleming et al. (1972) and Willig (1985) described it as being polyestrous, with birth periods occurring during the mid-dry season and during the mid-wet season. Furthermore, Tamsitt and Valdivieso (1963) reported *A. lituratus* as seasonally polyestrous. On the other hand, while in accordance with our findings *C. perspicillata* was described as having a unimodal reproductive phenology in Costa Rica (Stoner 2001), it has often been observed to have a bimodal reproduction pattern elsewhere (Mello et al. 2004; Ribeiro de Mello and Fernandez 2000; Charles-Dominique 1991; Ramirez-Pulido et al. 1993, La Val and Fitch 1977; Heithaus et al. 1975; Fleming et al. 1972). For *A. lituratus*, *A. obscurus*, and *C. perspicillata*, the presence of a high proportion of lactating females during the mid-wet season is consistent with a secondary pregnancy peak during the early wet season for which we lack capture data. Therefore, it cannot be excluded that even at the BDFFP these species may be seasonally polyestrous with a bimodal reproductive phenology. This hypothesis is further supported by the ability of *C. perspicillata* and *A. lituratus* to perform postpartum oestrus (Rasweiler and Badwaik 1997; Rodrigues et al. 2006). As suggested by Molinari and Soriano (2014), another hypothesis as to why these species experience geographic variation in their reproductive phenology is that the fruiting season is too short at our study site to allow species such as *C. perspicillata* to produce two offspring in this timeframe.

Compared with frugivores, the reproductive phenology of insectivorous phyllostomids is particularly poorly known. Durant et al. (2013), Dechmann (2005), and Estrada and Coastes-Estrada (2001) reported results ranging from seasonal monoestry and aseasonal monoestry to seasonal bimodal polyestry for different species. As in our study, *Trachops cirrhosus* was described as bimodally polyestrous by Sánchez-Hernández and Romero-Almaraz (1995) in Mexico. The reproductive phenology we observed in *Lophostoma silvicolum* at the BDFFP differs from observations made on all other species in our study, and its multimodal gestation does not match its unimodal lactation pattern. On Barro Colorado Island (Panama), *L. silvicolum* was observed to have two pregnancy peaks—one during the late dry season and another during the mid-dry season—and the species was suggested as being capable of postpartum estrus (Dechmann et al. 2005). Pregnant females may therefore be able to give birth when resources are at their maximum, e.g., during the

mid-dry season, explaining the presence of a single lactation peak for this species.

At the ensemble level, pregnancy of the frugivores was unimodal, and lactation was bimodal with peaks occurring during the late dry and mid wet seasons. However, as with *A. lituratus, A. concolor, C. brevicauda,* and *C. perspicillata,* the high proportion of lactating females captured in the late dry and mid wet season suggests that the frugivorous ensemble may have a bimodal reproductive phenology with a primary pregnancy peak occurring during the early wet season. This idea is supported by the fruiting peak in the early wet season at our study site (Haugaasen and Peres 2005, 2007; Bentos et al. 2008). Compared with frugivores, the gleaning animalivores displayed a more constant pregnancy phenology, with a high proportion of pregnant bats observed throughout the year, and lactation mostly concentrated during the dry period. In Costa Rica, this ensemble exhibited a single reproduction peak in the mid-late dry season (Durant et al. 2013), but the authors documented geographical variation in the reproductive strategy of gleaning animalivores: unimodal phenology was observed for this ensemble in Costa Rica while bimodal phenology was reported in northern South America and Mesoamerica (Durant et al. 2013). This difference in reproductive strategy may be due to smaller fluctuations in the availability of feeding resources for gleaning animalivores than for frugivores. Nonetheless our findings suggest that reproduction appears to be timed so that resources are abundant both when females are lactating and when pups are weaned, therefore maximizing the success of reproduction in both ensembles.

The ensemble-level phenology often does not correspond to the phenology of its component species. Mismatches of the reproductive phenology between specific species and their feeding ensemble are likely due to species-specific differences in preferred food resources and their temporal availability, or due to dietary flexibility associated with the capacity of complementing the diet with items typically associated with a different ensemble, e.g., consumption of insects by frugivorous bats or fruits for gleaning animalivores, therefore allowing species to exhibit more than one reproductive peak during a given season (Durant et al. 2013). In accordance, Estrada and Coates-Estrada (2001) reported that some frugivorous bat species with similar feeding habits may exhibit different reproductive phenologies due to differences in their preference for specific plant taxa (Dinerstein 1986), and by the differences in the fruiting phenology of these species (Laska 1990; Fleming et al. 1972). For instance, the timing of reproduction of *Cynopterus brachyotis* is strongly correlated with the timing of mango fruiting (Kofron 1997). Ecologically similar species that occur in sympatry may therefore exhibit different reproductive phenologies despite similar fruiting conditions (Stevenson et al. 2000).

Until now, few studies have illustrated the reproductive phenology of Neotropical bats. Species-level characterization of the pregnancy and lactation patterns are challenging due to considerable geographic biotic (timing and duration of resource availability) and abiotic (timing and duration of the rainy season) variation. However, such studies remain essential to better understand the biology of bats and the factors influencing their reproductive phenology. Fragmentation can affect the reproduction of some Neotropical bat species, often in a species-specific manner (de Oliveira et al. 2017) and leading to sex-specific responses to landscape features (Rocha et al. 2017a). Thus, it cannot be excluded that the phenology patterns observed at our study area are not influenced by fragmentation. Indeed, at a time when anthropogenic stressors such as fragmentation and global warming are increasingly influencing the reproductive behavior of a wide array of taxa (Klapwijk and Lewis 2008; Grazer and Martin 2012; Rocha et al. 2017a; Rossi et al. 2019) understanding which parameters modulate bat reproductive patterns can provide key conservation insights. Further long-term studies are paramount to investigate the reproductive behavior of bats, particularly across the tropics, where the reproductive phenology of most species remains unknown.

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Author contributions CM and RR conceived and designed the study. Data collection was performed by RR, ALB, FF and CM. Data analysis was performed by QH and JP. QH wrote the first draft and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Declarations

Conflict of interest The authors have no conflict of interest to declare.

Ethics approval This research was conducted under ICMBio (Instituto Chico Mendes de Conservação da Biodiversidade) permit (26877-2). All applicable institutional and/or national guidelines for the care and use of animals were followed.

Consent to participate Not applicable.

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