

Reproductive phenologies of phyllostomid bats in Costa Rica

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Reproductive phenologies of populations are strongly molded by environmental variation because natural selection favors individuals that time energetically demanding portions of their life cycle to correspond with periods of high resource availability. To evaluate how seasonal variation in abiotic characteristics and resources affects reproductive strategies, comparison among reproductive phenologies of species that use different resources and across geographic locations is crucial. To facilitate comparisons, it is essential to employ a rigorous and consistent classification scheme. Yet, few studies on the reproductive phenologies of bats, important seed dispersal and pollination agents in the tropics, have employed a clear or consistent classification scheme. We employed concise criteria to classify reproductive phenologies of frugivorous (*Artibeus jamaicensis*, *A. watsoni*, *Carollia castanea*, *C. perspicillata*, and *C. sowellii*) and nectarivorous (*Glossophaga soricina*) bat species, as well as 3 feeding ensembles of phyllostomids in northeastern Costa Rica. All 6 species exhibited bimodal phenologies (2 peaks). Each of the 3 ensembles exhibited different phenologies (i.e., frugivores: bimodal; nectarivores: polymodal [3 peaks]; and gleaning animalivores: unimodal [1 peak]). Bat species that consume plant material evinced pregnancy peaks in the late dry season and middle wet season, whereas gleaning animalivores exhibited a single peak in the middle to late dry season. Examination of geographic and temporal variation in phenologies revealed that strategies of frugivorous and nectarivorous species were geographically and temporally invariant, whereas strategies of gleaning animalivores differed among geographic locations.

Key words: Chiroptera, frugivores, gleaning animalivores, nectarivores, Neotropics, reproduction, seasonality

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Reproductive phenologies of populations are strongly shaped by environmental variation because natural selection favors individuals that time energetically demanding portions of their life cycle to correspond to periods of high resource availability (Bronson 1985). Anthropogenically induced global change may modify these phenologies by altering the timing of the resource availability or the timing of proximate cues that guide the initiation of reproductive behavior (i.e., mating). To detect and understand the effects of global change on plant and animal populations, the role of environmental variation must be understood in relation to reproductive phenologies, and extensive baseline data must be available for multiple species representing different guilds. Moreover, consistent criteria need to be applied in an unambiguous way to characterize phenologies so that long-term consequences of global change can be documented in an accurate manner.

Climate change and land-use change will most likely affect the abundance and distribution of species as well as the

ecological interactions among them (Aguirre et al. 2011). Bats, because of their diversity and role in many ecosystems, are bioindicators of such change because their responses to environmental variation reflect the responses of other taxa (Jones et al. 2009). The importance of bats may be greatest in the Neotropics, where they are locally the most species-rich mammalian group, attain high local abundance, and occupy a variety of ecological niches (Voss and Emmons 1996; Patterson et al. 2003). Neotropical bats play an integral part in the functioning of ecosystems because of the variety of foraging strategies that they employ, including frugivory, nectarivory, insectivory, and piscivory (Patterson et al. 2003). Moreover, bats provide an array of ecological services through seed dispersal, pollination, and regulation of insect populations



(Patterson et al. 2003), which facilitate forest regeneration (Heithaus et al. 1975; Shilton et al. 1999) and provide economic services such as agricultural pest control (Cleveland et al. 2006). Modifications of reproductive phenologies of Neotropical bats are of interest in their own right and are of additional interest because change in abundance of bats may affect the dynamics and sustainability of entire ecosystems (Jones et al. 2009).

Reproduction in bats may be more energetically demanding than in other terrestrial mammals (Kurta et al. 1989; Racey and Entwistle 2000). Consequently, it is critical that the most energetically expensive life-history events coincide with periods of high food resource productivity. Although gestation and lactation are both associated with increased energetic demands, daily energy expenditure is greater during lactation (Fleming 1988; Kurta et al. 1989). Additionally, the time during which juveniles are weaning is a critical period because of the high energy demands for growth while concurrently learning to forage (Handley et al. 1991).

For bats to time lactation and weaning with peaks in resource abundance, proximate cues are essential to initiate reproductive behavior. Potential cues known to influence reproduction in mammals are temperature, precipitation, humidity, and photoperiod (Bronson 1985). Manipulation of these variables using captive populations is an approach for understanding their importance in molding reproductive strategies. However, manipulative studies may not be applicable to free-ranging populations because it is difficult to include many energetic constraints (e.g., predator avoidance and evasion, foraging effort, and food quality) that interact with abiotic factors to affect reproductive phenologies. Assessment of geographic variation in reproductive phenologies across a variety of habitats may provide a means to evaluate the effects of these abiotic factors on reproductive strategies.

Although a number of studies have examined the reproductive phenologies of Neotropical bat species (Fleming et al. 1972; Wilson 1979; Willig 1985; Dinerstein 1986; Heideman et al. 1992; Ramírez-Pulido et al. 1993; Estrada and Coates-Estrada 2001; Stoner 2001; Zortea 2003; Dechmann et al. 2005; Tschapka 2005; Chaverri and Kunz 2006), research has not been evenly distributed among feeding guilds. Most work has focused on frugivorous or sanguivorous species (Wilson 1979; Dinerstein 1986; Heideman et al. 1992; Ramírez-Pulido et al. 1993; Stoner 2001; Zortea 2003; Chaverri and Kunz 2006). If insufficient sample sizes inhibit quantification of reproductive phenologies for species of other guilds, a solution is to combine reproductive data of all species within a particular feeding ensemble, and evaluate the general reproductive phenology of the group. This facilitates comparison among different feeding ensembles at a location and time period, in terms of general reproductive patterns and within-ensemble synchrony.

To facilitate comparisons of reproductive phenologies, it is essential to employ a rigorous and consistent classification scheme. The classification scheme should require sufficient sampling in most months of the annual cycle and precise

definitions of characteristics that distinguish peaks in reproductive activity. Some studies have been based on incomplete sampling throughout a year (e.g., Wilson 1979; August and Baker 1982) or on unclear criteria for defining reproductive phenologies (e.g., Dinerstein 1986; Ramírez-Pulido et al. 1993; Dechmann et al. 2005). To our knowledge, no study has outlined quantitative criteria to unambiguously distinguish among reproductive phenologies.

Accordingly, we employed concise criteria to classify reproductive phenologies of a number of phyllostomid species, as well as 3 feeding ensembles (i.e., frugivore, nectarivore, and gleaning animalivore ensembles). Additionally, we compared phenologies from this study to phenologies reported in the literature that had sufficient sample sizes throughout a year to explore the effects of geographic or environmental variation. Our main objective was to provide a rigorous and consistent classification scheme to facilitate comparisons of reproductive phenologies among species, across space, or over time.

MATERIALS AND METHODS

Study region and climate.—Bat reproduction was studied in a 175,000-ha region in the Caribbean lowlands of northeastern Costa Rica (10°25'53"N, 84°00'12.3"W). The study region comprises diverse land cover types including lowland wet tropical forests of various successional stages (e.g., old-growth and secondary forests), farms with a wide variety of crops, and cattle pastures. The climate is warm and moist, with relatively constant temperatures throughout the year and appreciable rainfall every month. The mean daily temperature is 31.0°C, with a range from 30.2°C to 31.9°C, and the average annual precipitation is 4,374.6 mm, with a range from 2,809.3 to 6,164.0 mm (Organization for Tropical Studies 2012). In general, a drier period occurs from January until late April, with mean monthly rainfall of 223.7 mm, followed by a wet period from early May to December, with mean monthly rainfall of 435.0 mm. Nevertheless, the dry and wet seasons during the years of this study (2009–2010) were less distinct (i.e., mean monthly rainfall was 353.8 mm in the dry season and 410.0 mm in the wet season [Fig. 1]).

Biological surveys.—Bats were surveyed on a monthly basis at 18 sites throughout the study region (Fig. 2) from August 2009 to September 2010; however, no sampling occurred in December 2009. Sites were positioned within forest patches that were embedded in a human-modified landscape. Sites were selected so that the area surrounding forested sites comprised a natural range in composition and configuration of land cover in the study region. On average, 14 sites were visited per month. Sampling effort was equivalent in all months with an average of 11,179 ($\pm 3,223$ SD) mist-net meter hours per month. For each survey, 12 ground-level mist nets (12 \times 2.5 m) were deployed within forested areas characterized by closed canopies. Generally, mist nets were opened for 6 h from dusk until midnight, and were continually inspected for bats every 30 min. However, some surveys ended prematurely because of severe weather because it increases health risks to

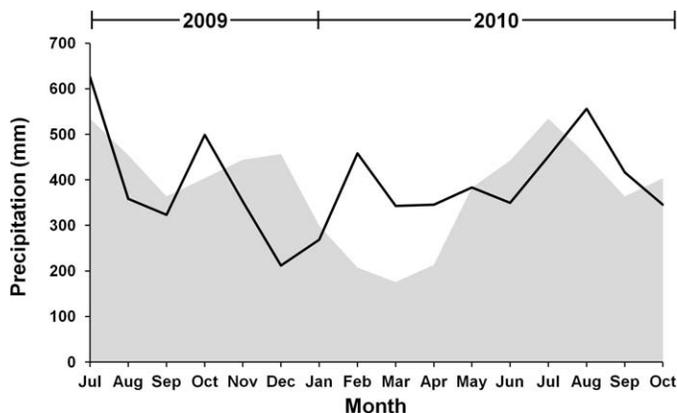


FIG. 1.—Average monthly precipitation from 1963 to 2010 (shaded area) and monthly precipitation during this study (July 2009 to October 2010) in northeastern Costa Rica ($10^{\circ}25'52.3''N$, $84^{\circ}00'12.3''W$ [Organization for Tropical Studies 2012]).

bats from exposure to low temperatures and rain. Sampling was not conducted during the presence of a moon that was $\geq 90\%$ full because of reduced bat activity associated with high lunar illumination (Morrison 1978). The protocol for animal use of this research followed the guidelines of the American Society of Mammalogists (Sikes et al. 2011), and was approved by the Institutional Animal Care and Use Committee (IACUC) at the University of Connecticut (IACUC number A09-014).

The species, sex, age, and reproductive state were recorded for each captured individual. To identify recaptures within a month, hair was trimmed on the back of each bat. Species were identified using a field key (Timm et al. 1999). Age was determined based on length of forearm and examination of the extent of ossification in the epiphyses of the phalanges (Timm et al. 1999). Reproductive classifications were restricted to adults. Pregnant females were identified via palpation; lactation was determined based on the condition of the mamma (i.e., evidence of hair loss and milk). Consequently, the number of nonreproductive females may be overestimated because small fetuses may be undetected without autopsy. Descended testes signaled reproductive activity in adult males.

Classification of reproductive phenologies.—We quantified reproductive phenologies at the levels of populations and ensembles. Classification of annual reproductive phenologies was primarily based on the number of peaks in the proportion of pregnant females in a population of a species or in populations of all species in a particular ensemble. For pregnancy or lactation, we classified peaks into 2 categories, primary and secondary. 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. Secondary peaks were defined as periods 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. High proportions of male reproductive activity were used to corroborate reproductive phenologies based on activity in females.

The number and timing of annual peaks in pregnancy or lactation distinguished among 4 phenological patterns: amodal, unimodal, bimodal, and polymodal reproduction. Amodal reproduction was distinguished by the absence of peaks in pregnancy or lactation, and the presence of reproductively active individuals in most months. Unimodal reproduction was identified by a single annual peak in pregnancy followed by a single peak in lactation. Multiple peaks in pregnancy (≥ 3), with each peak accompanied by a peak in lactation, characterized polymodal reproduction. Bimodal reproduction represents a special case of polymodal reproduction with only 2 peaks in pregnancy associated with 2 offset peaks in lactation. We were unable to distinguish between the 5 traditional reproductive phenologies (i.e., aseasonal monestry, aseasonal polyestry, seasonal monestry, seasonal bimodal polyestry, and seasonal polyestry [Fleming et al. 1972; Wilson 1979]) because data on the occurrence of single (monestrous) or multiple (polyestrous) estrous cycles were not documented in individuals from these populations. To determine the number of estrous cycles, either the annual number of pregnancies or lactation events in the same individual must be recorded, or individuals that are simultaneously pregnant and lactating must be documented in the population. When possible, we refined reproductive classifications based on species-specific information about estrous cycles from the literature. Reproductive phenologies were quantified for species and ensembles that had 5 or more adult females in at least 11 of the 13 surveyed months.

RESULTS AND DISCUSSION

Population-level phenologies.—Six species met the sampling requirement for classification of reproductive phenologies. All 5 frugivorous species (*Artibeus jamaicensis*, *A. watsoni*, *Carollia castanea*, *C. perspicillata*, and *C. sowelli*) as well as the 1 nectarivorous species (*Glossophaga soricina*) displayed a bimodal reproductive phenology (Fig. 3). Essentially, species exhibited a peak in pregnancy at the end of the dry season and a peak in pregnancy in the middle of the wet season; however, the particular month in which peaks occurred varied slightly among species. In general, peaks in pregnancy were followed 2 months later by peaks in lactation for each frugivorous species. For these species, high proportions of reproductively active males generally overlapped peaks in lactation and preceded peaks in pregnancy by a few months. Conversely, the reproductive pattern in males of the nectarivorous species, *G. soricina*, did not mirror the bimodal phenology of females. Rather, high proportions of males with descended testes were observed throughout most of the year, with the exception of the middle wet season. Asynchrony between periods of high reproductive activity in males and females may indicate that females are in estrus for extended periods with a concomitantly and protracted period of male activity (Handley et al. 1991).

Artibeus jamaicensis.—Peaks in pregnancy for *A. jamaicensis* occurred slightly earlier than for the other 4

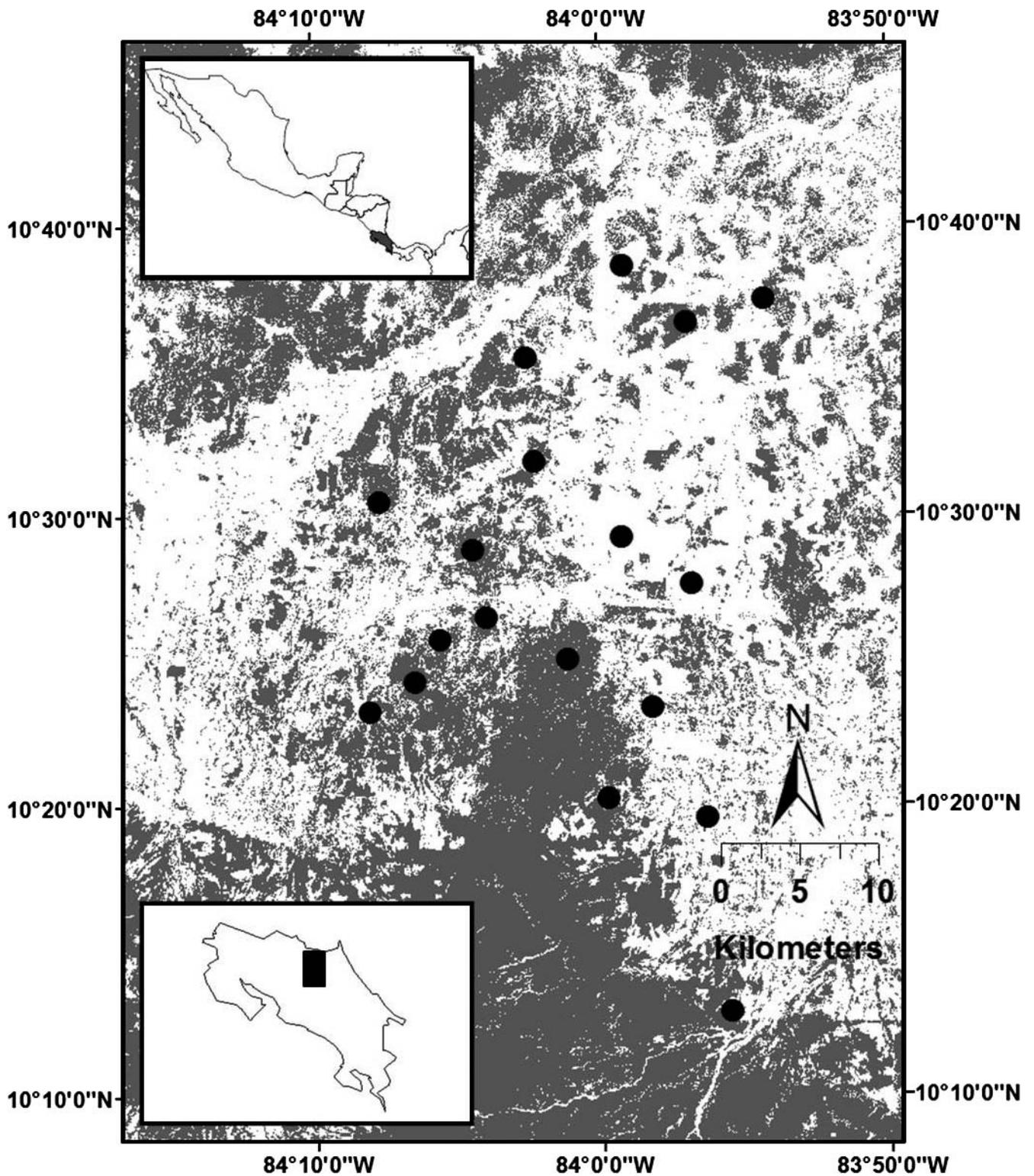


FIG. 2.—Location of 18 sampling sites (black dots). Forest land cover is displayed in gray whereas nonforest land cover is displayed in white. Location of Costa Rica (gray) in Central America is displayed in the upper-left corner of the map. Image in the lower-left corner shows location of the study area (black rectangle) in Costa Rica.

frugivorous species. The dry season peak in pregnancy occurred in March and the wet season peak occurred in July (Fig. 3a). Peaks in lactation occurred 2 months after each peak in pregnancy. We refine our classification of bimodal

reproduction of *A. jamaicensis* to be seasonal bimodal polyestry because individual females were documented to be simultaneously pregnant and lactating in Costa Rica (Mares and Wilson 1971) as well as at other geographic locations in

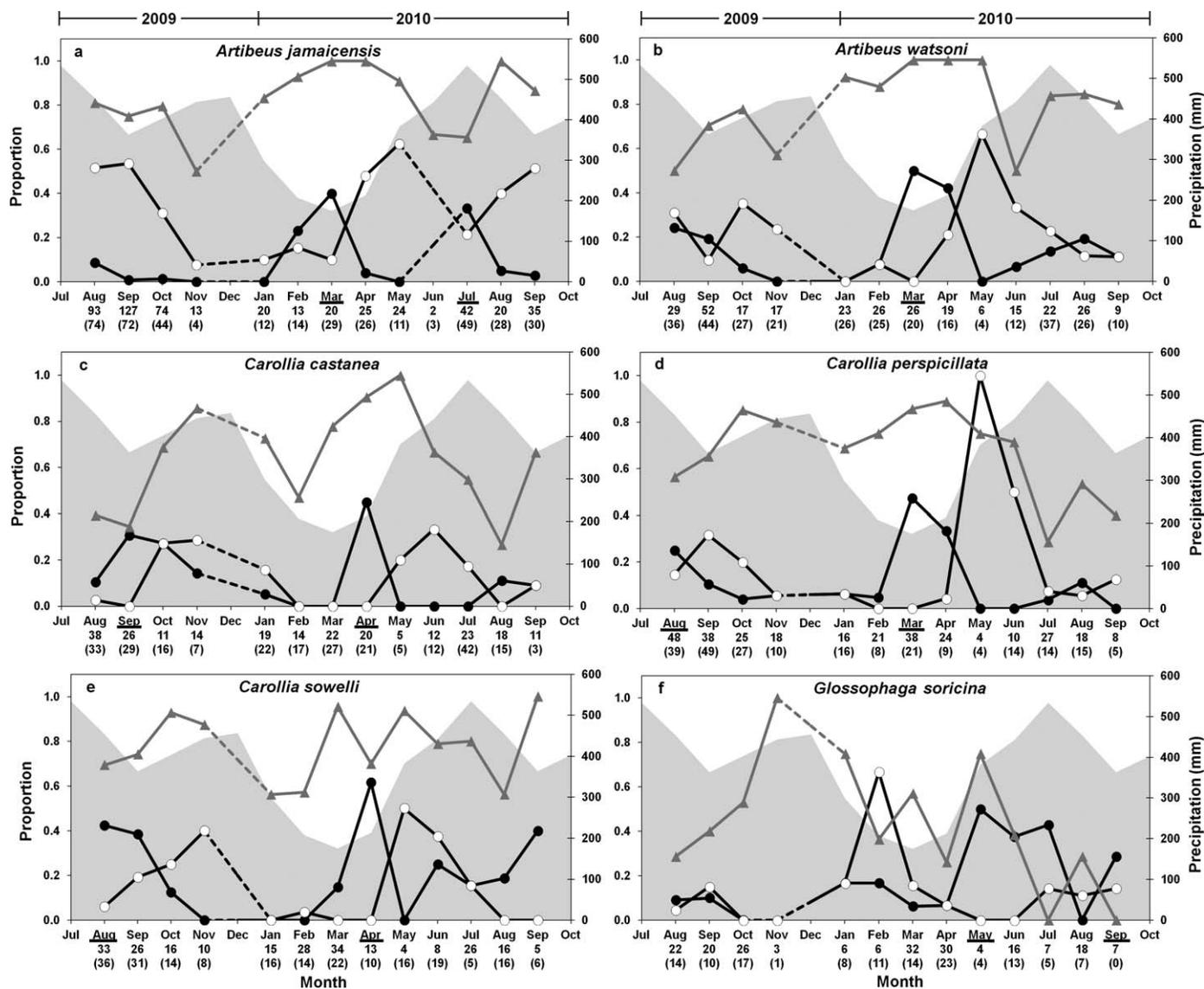


FIG. 3.—Graphical representations of reproductive phenologies of frugivorous and nectarivorous bat species from August 2009 to September 2010. Reproductive phenologies are based on monthly proportions of pregnant or of lactating females, and were corroborated by patterns of reproductive activity in males. Each species, a) *Artibeus jamaicensis*, b) *A. watsoni*, c) *Carollia castanea*, d) *C. perspicillata*, e) *C. sowelli*, and f) *Glossophaga soricina*, exhibits bimodal phenologies. Shaded background represents the average monthly precipitation for the study area from 1963 to 2010 (see Fig. 1). Filled circles represent monthly proportions of adult females that were pregnant. Open circles represent monthly proportions of adult females there were lactating. The number of captured adult females per month is indicated by a number (not parenthetical) below each month. Underlined months identify peaks in pregnancy. Filled gray triangles represent monthly proportions of adult males with scrotal testes. The number of captured adult males per month is indicated by parenthetical values below each month. Dashed lines provide trend estimates (i.e., means of adjacent months) for months with no sampling (December) or for months in which ≤ 2 individuals form the bases for estimates (i.e., June for *A. jamaicensis*).

Central and South America (Fleming et al. 1972; Willig 1985). Furthermore, observations of implanted blastocysts in lactating females of *A. jamaicensis* suggest postpartum estrus (Fleming 1971).

In general, the bimodal phenology of *A. jamaicensis* in northeastern Costa Rica was consistent with phenologies documented for this species at other geographic locations within Costa Rica (Fleming et al. 1972), and throughout Mesoamerica and northern South America (Fleming et al.

1972; Willig 1985; Handley et al. 1991; Ramírez-Pulido et al. 1993; Estrada and Coates-Estrada 2001) despite variation in climate and vegetation among studies. Bimodal reproduction of *A. jamaicensis* at other geographic locations was characterized by a peak in the dry season and another in the wet season; however, timing of peaks within the seasons (i.e., early, middle, or late) was variable among locations. Only a single study with sufficient sample sizes reported reproductive phenologies for *A. jamaicensis* that differed from bimodal

reproduction in the dry forest of northwestern Costa Rica (i.e., unimodal reproduction—Stoner 2001). The phenological differences among geographic locations may be due to the degree to which abiotic conditions and resource availability differ among locations. Indeed, in the absence of seasonal variation in critical environmental characteristics, the reproductive phenologies of wild-caught but captive populations tend toward ones characterized with shorter interbirth intervals (Handley et al. 1991). The longer interbirth interval of populations from northwestern Costa Rica than of those of populations from northeastern Costa Rica may be attributed to the stark contrast between the dry season (~ 50.9 mm rain per month—Frankie et al. 1974) and wet season (~ 215.6 mm rain per month—Frankie et al. 1974) of northwestern Costa Rica compared to that of northeastern Costa Rica.

Artibeus watsoni.—The reproductive phenology of *A. watsoni* exhibited a peak in pregnancy in the late dry season (March) and a distinct increase in the proportion of pregnancies in the middle of the wet season (August [Fig. 3b]). Because of the presence of a peak in lactation in October, following the increase in the proportion of pregnant females, we inferred the existence of a secondary peak in pregnancy in August. Similar to *A. jamaicensis*, peaks in lactation occurred 2 months after peaks in pregnancy. Bimodal reproduction of *A. watsoni* also was observed in lowland tropical forests of southwestern Costa Rica (Chaverri and Kunz 2006) and of Panama (Fleming et al. 1972). A peak in pregnancy occurred in the dry season and in the wet season; however, timing of peaks within the seasons (i.e., early, middle, or late) differed among studies. Annual reproductive phenologies of *A. watsoni* are not available for other locations throughout its geographic range (i.e., southern Mexico to southwestern Colombia—Simmons 2005).

Carollia castanea.—The peaks in pregnancy (in April and in September) of *C. castanea* (Fig. 3c) occurred later than did those of the species of *Artibeus* (Figs. 3a and 3b). Peaks in lactation occurred 1–2 months following the peaks in pregnancy. The phenology of *C. castanea* was previously documented in the Caribbean lowlands of Costa Rica (LaVal and Fitch 1977) and in Panama (Fleming et al. 1972). The phenologies in those studies were consistent with that in this study in that peaks of pregnancy occurred in the late dry season and in the middle wet season. Reproductive phenologies of *C. castanea* are not known at other locations within its geographic range (i.e., Honduras to Peru, Bolivia, western Brazil, and Venezuela—Simmons 2005).

Carollia perspicillata.—The timing of peaks in pregnancy of *C. perspicillata* (Fig. 3d) was similar to those of *Artibeus* (Figs. 3a and 3b). Periods of lactation occurred 1–2 months after peaks in pregnancy, although the period of lactation in September was not strictly considered a peak by our classification scheme because of the large primary peak in lactation in May. Simultaneous pregnancy and lactation were previously documented in *C. perspicillata* from populations in Costa Rica (Mares and Wilson 1971; Fleming et al. 1972) as well as in the semiarid Caatinga and edaphic Cerrado of northeastern Brazil (Willig 1985). Additionally, females from

captive colonies of *C. perspicillata* became pregnant 28–32 days postpartum, and successfully reared young while pregnant (Laska 1990; Rasweiler and Badwaik 1997). Accordingly, we refined our classification of bimodal reproduction to seasonal bimodal polyestry.

Nearly all annual reproductive phenologies of *C. perspicillata* in Central and South America are bimodal with a peak in pregnancy in the dry season and in the wet season (Fleming et al. 1972; LaVal and Fitch 1977; Willig 1985; Mello et al. 2004). Similar to the other frugivorous species, timing of peaks within the dry and wet seasons (i.e., early, middle, or late) varied geographically. Only a single study with sufficient sample sizes reported a phenology different from bimodal phenology (Stoner 2001). Unimodal reproduction was exhibited by *C. perspicillata* in the dry forest of northwestern Costa Rica. The long and severe dry season and relatively short growing season of this region compared to the Caribbean lowlands of northeastern Costa Rica (Frankie et al. 1974) most likely restricts the number of reproductive events within a year.

A variety of environmental cues likely drive reproductive phenologies in *C. perspicillata*. Indeed, in the absence of environmental cues, pregnancies of captive populations became asynchronous (Laska 1990). One reproductive cue may be the transition of immature fruits to mature fruits of *Piper*, a main food source of *C. perspicillata*. This transition was associated with peaks in pregnancy of *C. perspicillata* in montane forest of Bolivia (Barboza-Márquez and Aguirre 2010). Using path analysis, Mello et al. (2004) characterized the direct and indirect effects of variation in abiotic factors and resources on the reproductive phenology of *C. perspicillata* in southeastern Brazil. Although the timing of *Piper* production had the greatest direct effect on reproduction, temperature had the strongest indirect effect. Similar analyses are needed throughout the geographic distribution of this species to understand the factors that mold phenological patterns of reproduction.

Carollia sowelli.—Months with peaks in pregnancy of *C. sowelli* (Fig. 3e) occurred between months with peaks in pregnancy of the other species of *Carollia* (Figs. 3c and 3d), and were followed by peaks in lactation 1–3 months later. *C. sowelli* was recently distinguished from *C. brevicauda*, and ranges from central Mexico to western Panama, whereas *C. brevicauda* is distributed from eastern Panama to Bolivia (Baker et al. 2002). Accordingly, reproductive phenologies reported for *C. brevicauda* from Mexico to western Panama pertain to *C. sowelli*. Thus, bimodal reproduction has been documented for *C. sowelli* in the Caribbean lowlands of Costa Rica (LaVal and Fitch 1977) as well as in the tropical forests of southern Mexico (Estrada and Coates-Estrada 2001).

Glossophaga soricina.—The nectarivorous species, *G. soricina*, displayed peaks in pregnancy (Fig. 3f) that occurred later than did those of the frugivorous species (Figs. 3a–e). Each peak in pregnancy was not followed by a discernible peak in lactation. Instead, a single peak in lactation occurred in February; however, this peak is based on a small sample (i.e., 4 of 6 individuals).

TABLE 1.—Species composition of 3 ensembles of phyllostomid bats from the Caribbean lowlands of northeastern Costa Rica.

Frugivores	Nectarivores	Gleaning animalivores
<i>Artibeus jamaicensis</i>	<i>Glossophaga commissarisi</i>	<i>Lonchorhina aurita</i>
<i>Artibeus lituratus</i>	<i>Glossophaga soricina</i>	<i>Lophostoma brasiliense</i>
<i>Artibeus phaeotis</i>	<i>Hylonycteris underwoodi</i>	<i>Lophostoma silvicolium</i>
<i>Artibeus watsoni</i>	<i>Lichonycteris obscura</i>	<i>Miconycteris hirsuta</i>
<i>Carollia castanea</i>	<i>Lonchophylla robusta</i>	<i>Miconycteris microtis</i>
<i>Carollia perspicillata</i>	<i>Phyllostomus discolor</i>	<i>Miconycteris schmidtorum</i>
<i>Carollia sowelli</i>		<i>Mimon crenulatum</i>
<i>Chiroderma villosum</i>		<i>Phyllostomus hastatus</i>
<i>Ectophylla alba</i>		<i>Tonatia saurophila</i>
<i>Mesophylla macconnelli</i>		<i>Trachops cirrhosus</i>
<i>Platyrrhinus helleri</i>		<i>Trinycteris nicefori</i>
<i>Sturnira lilium</i>		
<i>Uroderma bilobatum</i>		
<i>Vampyressa nymphaea</i>		
<i>Vampyressa thuyone</i>		

The geographic documentation of annual reproductive phenologies of *G. soricina* is extensive. Throughout Mesoamerica in Mexico, El Salvador, Costa Rica, and Panama (Felten 1956; Fleming et al. 1972; Ramírez-Pulido et al. 1993; Estrada and Coates-Estrada 2001; Stoner 2001) as well as in Brazil (Willig 1985; Zortea 2003), reproductive phenologies are bimodal with a peak in pregnancy in the dry season and another in the wet season. Nonetheless, timing of peaks within a season (i.e., early, middle, or late) varied geographically. Although the reproductive phenology of *G. soricina* has not been previously documented in the Caribbean lowlands of Costa Rica, the phenology of a sister species, *G. commissarisi*, from this area is consistent with the bimodal pattern observed in *G. soricina* (LaVal and Fitch 1977; Tschapka 2005).

Ensemble-level phenologies.—Three feeding ensembles met the sampling requirement for classification of reproductive phenologies (Table 1). The frugivore, nectarivore, and gleaning animalivore ensembles each exhibited different reproductive phenologies (Fig. 4). The phenologies of an ensemble result from a combination of phenologies of populations of different species and are weighted by species-specific monthly abundances. The reproductive phenology of the ensemble will be an artifact if the constituent species exhibit phenologies that are not synchronized.

Frugivores.—The frugivore ensemble comprised 15 species (Table 1) and exhibited a bimodal phenology (Fig. 4A). The primary peak of pregnancy occurred at the end of the dry season (March and April), followed by a secondary peak in the middle of the wet season (August). Peaks in lactation were observed 1 month after each pregnancy peak. High proportions of reproductively active males occurred during peaks in lactation and preceded peaks in pregnancy by a few months.

Because the reproductive phenologies of frugivorous species were highly synchronized, it is critical that periods of lactation and weaning coincide with periods of high resource produc-

tivity to optimize reproductive output and survivorship of offspring. The prime fruiting period in Caribbean lowlands of northeastern Costa Rica occurs from August through October (Frankie et al. 1974) and is coincident with the wet season peak in lactation in September (Fig. 4A). In the dry season and early wet season, Lopez and Vaughan (2007) found that monthly proportions in pregnancy and lactation of frugivorous bat species from the Caribbean lowlands of Costa Rica were more correlated with monthly proportions of arthropods and *Vismia panamensis*, a species that produces fruit in the dry season (Tschapka 2004), rather than with other components of their diets (e.g., *Cecropia*, *Piper*, and *Ficus*). Arthropods are high energy and high protein sources. The consumption of arthropods by bats may be especially critical during peaks in lactation (Lopez and Vaughan 2007). Arthropod abundance generally is greatest shortly after peaks in leaf flushing (Boinski and Fowler 1989), which would coincide with the peak in lactation of frugivorous species (i.e., May [Fig. 4A]) during the late dry and early wet season of the Caribbean lowlands of Costa Rica (Frankie et al. 1974). Furthermore, diets of frugivorous species comprise a greater number of fruit species during the dry season than during the wet season (Lopez and Vaughan 2007). Accordingly, energetic demands of lactation at the beginning of the wet season (Fig. 4A) may be satisfied via increased arthropod abundance and expansion of the fruit diets of frugivorous species.

Nectarivores.—The nectarivore ensemble comprised 6 species (Table 1) and exhibited a polymodal phenology (Fig. 4B). Peaks in pregnancy occurred in February, July, and September. This phenology was corroborated by 3 periods with high proportions of reproductively active males that generally occurred 2–3 months before peaks in pregnancy. Interestingly, there were only 2 peaks in lactation; 1 overlapped a peak in pregnancy in February. The concurrent peaks in pregnancy and lactation suggest that peaks in reproductive activity of different species occur at different times of the year. Indeed, considerable interspecific variation characterized reproductive activity. For example, the peak in pregnancy in July is due to pregnant females of *G. soricina* and *Hylonycteris underwoodi*, whereas the peak in September is due to *G. soricina* and *G. commissarisi*, suggesting that the ensemble-wide pattern is an artifact.

One explanation for nonsynchronized phenologies among nectarivorous species is that they use different food resources. Greatest asynchrony among peaks occurred in the wet season. Flowering by plants available to bats occurs from the middle wet season to the middle dry season in the Caribbean lowlands of Costa Rica (i.e., September–March—Tschapka 2004). Accordingly, the diets of nectarivorous species are dominated by nectar and pollen from August to the end of February (Tschapka 2004, 2005). Although some plant species are eaten by many nectarivorous species, some plant species are primarily consumed by a single bat species (Tschapka 2004). For example, *G. commissarisi* feeds on *Cecropia* spp. and *Matisia cordata* significantly more than does *H. underwoodi*. *H. underwoodi* consumes nectar from epiphytes (i.e., *Maekea*

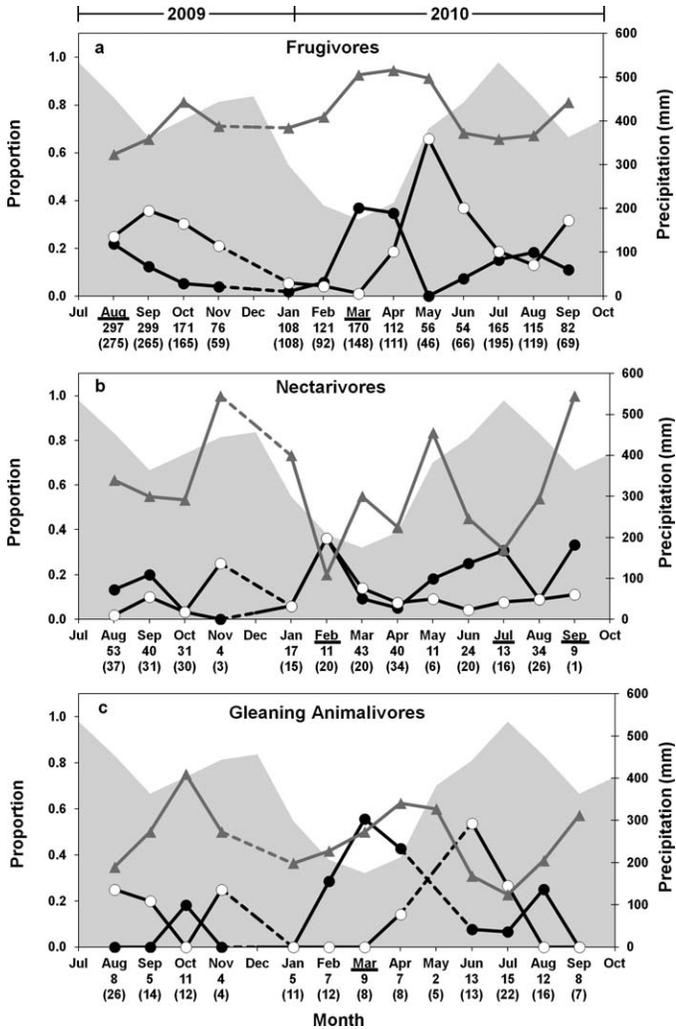


FIG. 4.—Graphical representations of reproductive phenologies of 3 phyllostomid bat ensembles from August 2009 to September 2010. Reproductive phenologies are based on monthly proportions of pregnant or of lactating females, and were corroborated by patterns of reproductive activity in males. A) Frugivores exhibit a bimodal phenology; B) nectarivores exhibit a polymodal phenology; and C) gleaning animalivores exhibit a unimodal phenology. Shaded background represents the average monthly precipitation for the study area from 1963 to 2010 (see Fig. 1). Filled circles represent monthly proportions of adult females that were pregnant. Open circles represent monthly proportions of adult females that were lactating. The number of captured adult females per month is indicated by a number (not parenthetical) below each month. Underlined months identify peaks in pregnancy. Filled gray triangles represent monthly proportions of adult males with scrotal testes. The number of captured adult males per month is indicated by parenthetical values below each month. Dashed lines provide trend estimates (i.e., means of adjacent months) for months with no sampling (December) or for months in which ≤ 2 individuals form the bases for estimates (i.e., May for gleaning animalivores).

neurantha, *Marcgravia* spp., and *Weberocereus tunilla*) and some trees (i.e., *Quararibea parvifolia* and *Matisia bracteolosa*) significantly more than does *G. commissarisi* (Tschapka 2004). Thus, plant–pollinator coevolution and interspecific

competition among plants may give rise to different flowering phenologies leading to asynchrony of peaks in pregnancy by bat pollinators.

Gleaning animalivores.—The gleaning animalivore ensemble comprised 11 species (Table 1) and exhibited a unimodal phenology (Fig. 4C). A single peak in pregnancy occurred during the dry season (March), followed by a peak in lactation during the wet season (June). For each species, pregnancies occurred in the middle to late dry season. Similarly, females from many species were lactating in the early wet season. This suggests that a unimodal phenology is a general pattern for gleaning animalivores in the Caribbean lowlands of Costa Rica. Males were reproductively active for several months before the peak in pregnancy. High proportions of males with descended testes occurred at the end of the dry season (April and May) and at the end of the wet season (September and October).

A few studies have documented annual reproductive phenologies of gleaning animalivores (Willig 1985; Estrada and Coates-Estrada 2001; Dechmann et al. 2005). Pregnant and lactating *Pteronotus parnellii* from the Caribbean lowlands of Costa Rica (LaVal and Fitch 1977) support the contention of unimodal pattern for the ensemble; however, sample sizes were small. Nevertheless, a bimodal phenology more commonly occurs in Mesoamerica and northern South America, with a peak in pregnancy in the dry season and another in the wet season (Willig 1985; Estrada and Coates-Estrada 2001; Dechmann et al. 2005). Arthropod abundance generally is greatest in the late dry and early wet seasons in the Caribbean lowlands of Costa Rica, and may supply the energetic demands of multiple species of gleaning animalivores. A secondary peak in pregnancy in the wet season may be unique to some species because of species-specific use of resources apart from arthropods.

Implications.—The effects of abiotic characteristics and resources on reproductive phenologies remain poorly understood; however, comparison among studies from different geographic regions or among studies from the same area but under changed environmental conditions provide fruitful insights. In general, the reproductive phenologies of frugivorous and nectarivorous species were geographically invariant, whereas the strategies of the gleaning animalivores differed among geographic locations.

For frugivorous and nectarivorous species, bimodal phenology occurred throughout Mesoamerica and northern South America, although the timing of reproductive peaks within the dry and wet seasons were geographically variable (Felten 1956; Fleming et al. 1972; Willig 1985; Handley et al. 1991; Ramírez-Pulido et al. 1993; Estrada and Coates-Estrada 2001; Zortea 2003). The only instance of a nonbimodal phenology occurred in northwestern Costa Rica, where populations of *A. jamaicensis* and *C. perspicillata* exhibited a single reproductive peak (Stoner 2001). Northwestern and northeastern Costa Rica differ in the amount of precipitation and the seasonal contrast of environmental characteristics (Frankie et al. 1974). More specifically, seasonal variation of northwestern Costa

Rica is characterized by a dramatic shift from a very hot and dry climate to relatively wet and cooler climate, whereas variation in temperature and precipitation in northeastern Costa Rica is more subtle and the climate is wet year-round (Frankie et al. 1974). The long and severe dry season and relatively short growing season of northwestern Costa Rica may limit the number of reproductive pulses that can occur within a year.

A comparison of results from 2009 to 2010 (this study) and 1973 to 1974 (LaVal and Fitch 1977) provides insight into the extent to which global change during the intervening ~30 years has altered reproductive phenologies of bats in the Caribbean lowlands. The climate of the study area has become warmer and wetter over the past 30 years (Whitfield et al. 2007), and the landscape has been appreciably modified for human land use (Joyce 2006). Nevertheless, reproductive phenologies of *C. castanea*, *C. perspicillata*, and *C. sowelli* are indistinguishable between these time periods. Increasing precipitation and pervasive human land use had little effect on contemporary reproductive phenologies. Although habitat loss and fragmentation increase the energetic cost of foraging for forest core species (i.e., species have to travel to many forest patches to acquire resources), fragmentation increases resource abundance for gap-specialist species that consume early successional plants. Many species of *Carollia* primarily consume *Piper*, an early successional plant (Lopez and Vaughan 2007). Accordingly, moderate forest loss and fragmentation may have little effect on their reproductive strategies. Nonetheless, extrapolation of results from relatively short-duration studies to predict longer-term trends should be done with caution. Indeed, repeated short-term studies or longer-term studies using consistent and rigorous criteria are required for predictive understanding.

Although considerable research has clarified the ecology and behavior of bats (Kunz and Fenton 2003), little work has concentrated on reproductive phenologies. To better understand how environmental variation, including climate change and land-use change, affects reproductive strategies of bats, annual reproductive phenologies must be quantified in a variety of habitats across geographic ranges of species, especially for nonfrugivorous species. Furthermore, it is critical that future studies use a consistent classification scheme to facilitate comparisons so as to detect alteration in phenology that may ramify throughout tropical food webs.

RESUMEN

Los patrones reproductivos de las poblaciones se ven afectados por la variabilidad en el ambiente. La selección natural favorece a los individuos que sincronizan las fases de su ciclo de vida que son energéticamente costosas con los periodos de alta disponibilidad de recursos. Para evaluar como la variación estacional en factores abióticos y recursos afecta las estrategias reproductivas, es vital realizar comparaciones entre los patrones reproductivos de especies que usan diferentes recursos y diferentes ubicaciones geográficas. Para facilitar comparaciones, es esencial emplear un esquema de clasificación riguroso y constante. Sin embargo, muy pocos

estudios sobre fenologías reproductivas de murciélagos, los cuales son agentes importantes de polinización y dispersión de semillas en los bosques tropicales, han empleado esquemas de clasificación claros o consistentes. En el presente estudio, empleamos criterios concisos para clasificar las fenologías reproductivas de 5 especies de murciélagos frugívoros (*Artibeus jamaicensis*, *A. watsoni*, *Carollia castanea*, *C. perspicillata*, y *C. sowelli*), un murciélago nectarívoro (*Glossophaga soricina*), y 3 ensamblajes de phyllostomidos en el noreste de Costa Rica. Las 6 especies exhibieron patrones bimodales (2 picos). Cada uno de los ensamblajes mostro diferentes patrones reproductivos (i.e., frugívoros: bimodal; nectarívoros: polimodal [3 picos]; y insectívoros de follaje: unimodal [1 pico]). Las especies de murciélagos que se alimentan de material vegetal, mostraron picos de gestación al final de la estación seca y a mediados de la estación lluviosa, mientras que los insectívoros de follaje muestran solamente un pico de gestación a mediados de la estación seca. Los patrones reproductivos de las especies de murciélagos frugívoros y nectarívoros no se ven afectados por la variación geográfica y temporal, mientras que las estrategias usadas por los murciélagos insectívoros de follaje muestran diferencias entre distintas ubicaciones geográficas.

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