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Seasonality and synchrony of reproduction in three species of nectarivorous Philippines bats

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Abstract

Background: Differences among species and among years in reproductive seasonality (the tendency for clusters of events to fall at approximately the same point in each year) and synchrony (amount of clustering of events within a year) have been intensively studied in bats, but are difficult to assess. Here, we use randomization methods with circular statistics to test for synchrony and seasonality of reproduction in three species of nectarivorous megachiropteran bats on Negros Island in the central Philippines.

Results: In *Rousettus amplexicaudatus*, estimated dates of birth were both highly synchronous and highly seasonal. In *Macroglossus minimus*, estimated births were seasonal and significantly clustered within years, but within each year births occurred over a broad period, indicating a low level of synchrony. In *Eonycteris spelaea*, estimated births were also seasonal and had statistically significant synchrony, with birth periods within years intermediate in synchrony between *R. amplexicaudatus* and *M. minimus*. All three species had a similar seasonal pattern, with two birth periods in each year, centered on March or April and August or September. In one species, *R. amplexicaudatus*, primigravid females (in their first pregnancy) produced their young in June and July, a birth period significantly different in timing from the two birth periods of older adult females. This more conservative pattern of young females may allow higher survival of parents and offspring at cost of a lost reproductive opportunity. There was weak evidence that in some years primigravid females of *M. minimus* might differ in timing from older adults. There were few significant differences in reproductive timing among different years, and those differences were generally less than two weeks, even during a severe drought in the severe el Niño of 1983.

Conclusion: The results suggest that these species follow an obligately seasonal pattern of reproductive timing with very little phenotypic plasticity. The resampling methods were sensitive to differences in timing of under two weeks, in some cases, suggesting that these are useful methods for analyses of seasonality in wild populations of bats.

Background

Seasonality in the timing of bat reproduction and other life-history events is common in most terrestrial habitats [1]. The selective pressure favoring seasonal reproduction

is the reduction in reproductive success during the harsher seasons [2]. This selection pressure for seasonality is opposed by the fitness cost of foregoing the opportunity to reproduce. At least five major factors affect the degree

of seasonality of reproduction in a species: life expectancy [3], cost of reproduction, severity of the harsh season, predictability of the harsh season, and the accuracy and precision of an individual's ability to estimate time of year. If selection favors a pattern of reproductive timing that maximizes fitness, then fitness trade-offs from these factors may affect the degree of synchrony and seasonality of reproduction. Here we define synchrony as similarity in timing of events within a population within a year and seasonality as similarity in the mean timing of events in a population among multiple years. Seasonal and highly synchronous reproduction should be favored if there is a single, narrow window offering optimum conditions for reproduction [4]. The degree of both synchrony and seasonality may be affected by such factors as temporal peaks in resources, predator satiation, advantages of intra-specific cooperation (e.g., clustering of juveniles for warmth), or intra/interspecific competition. There is a broad range of temporal reproductive strategies among mammals both within and among species [1,2], which may indicate that there are many potential solutions to these trade-offs.

Seminal papers by Baker and colleagues in the 1930's demonstrated that seasonal reproduction occurs in tropical bat species, and suggested that seasonal changes in weather conditions resulting in seasonal changes in food might cause this seasonal reproduction [5,6]. Other potential causes for seasonality include seasonal changes that may be unrelated to seasonal weather conditions, including seasonal changes in ease of obtaining food, seasonal changes in competition, and seasonal changes in predation pressures. These selective pressures may favor timing the periods of pregnancy, lactation, or weaning during periods when conditions are least harsh [7,8]. In the decades since Baker's work, evidence has accumulated that most tropical bats reproduce seasonally, and much of the evidence suggests that seasonal climate patterns are a major cause of seasonal reproduction of tropical bats [1].

Many hypotheses have been proposed to account for patterns of reproductive timing in bats (reviewed by [1,9]). These hypotheses often differ in their predictions for timing of births (for example, predicting that births should coincide with a particular season or should coincide with life history events of some other species, or predicting that reproduction should or should not be synchronous). Thus, it would be useful to be able to use field data on pregnancy to test whether the timing of births is different in two different populations or in two different years, when we know, for example, that the timing of a wet season or of spring differs between the two populations or the two years.

However, it remains challenging to distinguish among hypotheses about the causes of seasonality in specific

cases. In analyzing patterns of seasonality in bat communities, tests of hypotheses are difficult, in part because most accounts either make comparisons without the use of statistics or make statistical comparisons of proportional data (e.g., proportion pregnant or proportion lactating). In the latter case, when data are reduced to information on the proportion of females that are pregnant or lactating, statistical testing can be carried out, but precise estimation of the mean and variance of birth dates is no longer possible. This mode of analysis reflects the absence of any acceptable, better alternative to analysis of the data sets from typical field studies on bat reproduction. Ideally, statistical methods should allow estimation of birth dates with a mean and variance, and allow use of these kinds of data to compare timing of reproduction in a single population from year to year or compare different populations or species in a single year.

Here, we use resampling methods [10-12] with circular statistics [13] to assess synchrony and seasonality of reproduction in a nectarivore, Megachiropteran bat community from the Central Philippines. Using methods modified from those developed by Heideman [9] we compare reproductive timing between age classes, among years, and among species. The objectives were to (1) test for seasonality and synchrony in the timing of births within each species, (2) test for evidence for age-specific reproductive strategies within species [14], and (3) test the hypothesis that all three species of nectarivore follow the same seasonal strategy. The resampling methods were found to be an improvement over previous analytical approaches, as significant synchrony and seasonality of births were identified and some significant differences were observed between age classes or years. However, there are also some problems with the use of these statistical methods.

Results

Births of multiparous adult female *R. amplexicaudatus* were significantly clumped in two well-defined clusters per year, one in March/April and the other in August/September (Fig. 1a & 1c, Table 2). Most females captured in April and May were lactating as well as pregnant (e.g., Fig. 1a showing 1983), indicating that most and probably nearly all female *R. amplexicaudatus* have young in both birth periods. In all years for which data were sufficient for analysis, clusters in both periods (Fig. 1c) were highly statistically significant (Table 2). The timing of these clusters differed slightly between some years (6 of 18 pairwise comparisons). Births in the August/September cluster of 1991 were significantly earlier than in 1982, 1983, 1987, and 1992 ($p < 0.05$ for all) by an average of 1 – 2 weeks.

Primigravid young female *R. amplexicaudatus* (those in their first pregnancy) were significantly clustered in births,

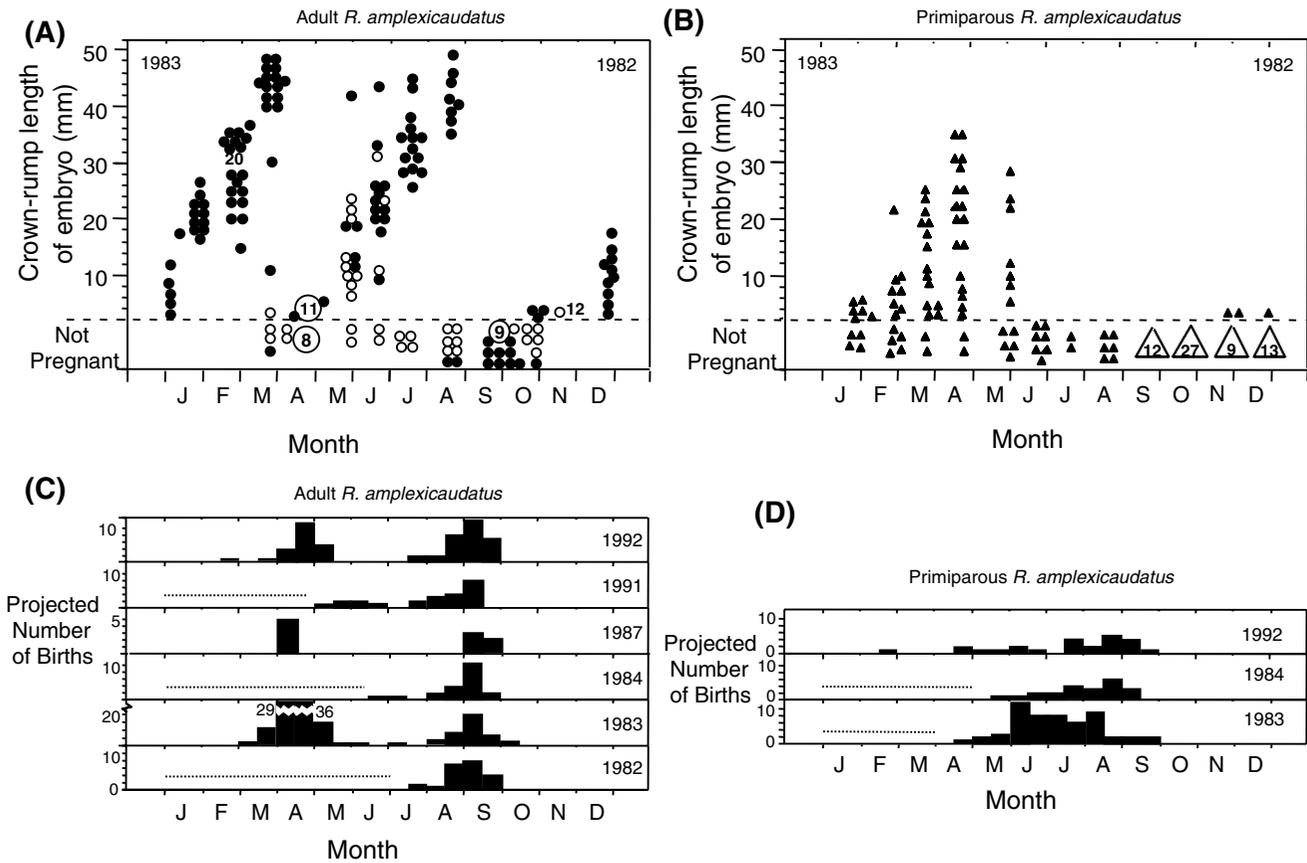


Figure 1
Reproductive status of *Rousettus aplexicaudatus*. (a) Sample data showing parous adult females from June 1982 to July 1983 (these months have been rearranged for display to show January to December for consistency with other figures). (b) Primigravid females from June 1982 to July 1983 (these months have been rearranged to display January to December). (c) Estimated timing of births in parous adults collected from 1982 to 1992. (d) Estimated timing of births in primigravid females collected from 1982 to 1992. In (a), open circles indicate individuals lactating, solid circles indicate individuals not lactating, circles enclosing numerals indicate that number of females lactating, and numerals alone indicate that number of individuals not lactating. In (b), solid triangles indicate individual females, triangles enclosing numerals indicate that number of females. Dashed lines in (c) indicate no data available.

Table 1: Approximate gestation length, embryo crown-rump length (C-R) at birth, and duration of lactation in three species of nectarivorous Pteropodids. Data on approximate crown-rump length at birth are from this study, as are the estimates of the duration of gestation and lactation for *R. aplexicaudatus*. Estimates of gestation and lactation for *M. minimus* are from Start [26]; estimates for *E. spelaea* are based on Bhat et al. [56].

| Species | Gestation | C-R at Birth | Lactation |
|---------------------------------|-----------|--------------|-----------|
| <i>Rousettus aplexicaudatus</i> | 150 days | 47 mm | 60 days |
| <i>Macroglossus minimus</i> | 120 days | 28 mm | 65 days |
| <i>Eonycteris spelaea</i> | 120 days | 44 mm | 60 days |

Table 2: Clusters in estimated births in *Rousettus amplexicaudatus* and *Macroglossus minimus*. Data in early 1992 were adequate for testing for synchrony of births in *M. minimus*, but, because of truncation, not for accurately estimating the midpoint of peaks; therefore, only significance levels are shown in those cases. One case that was near statistical significance (bordered by parentheses) is shown with the attained p value. (ns indicates nonsignificance; blank space indicates no data; * = $p < 0.05$; ** = $p < 0.01$; * = $p < 0.001$).**

| Year | <i>Rousettus amplexicaudatus</i> | | <i>Macroglossus minimus</i> | |
|-------|----------------------------------|-------------|-----------------------------|-----------------|
| | Parous Adult | Primigravid | Parous Adult | Primigravid |
| 1982b | 30 Aug *** | | 28 Sept ** | ns |
| 1983a | 10 Apr *** | | 23 Mar *** | 3 May * |
| 1983b | 26 Aug *** | 2 Jul *** | 10 Aug *** | 7 Aug *** |
| 1984 | 19 Aug *** | 24 Jul *** | 18 Aug * | 1 Sept *** |
| 1987a | 28 Mar *** | | ns | ns |
| 1987b | 2 Sept *** | | 9 Aug *** | (28 Aug; 0.055) |
| 1991 | 15 Aug *** | | ns | 23 Aug ** |
| 1992a | 20 Apr *** | | ** | * |
| 1992b | 25 Aug *** | 19 Jul *** | ns | |

with a broad peak of births from June to late August in the three years for which data were sufficient for analysis (Fig. 1b & 1c, Table 2). Births from primigravid females were also seasonal, as there were no significant differences in the timing of births of primigravid females among years. The single annual cluster of births in these young adult females fell between and was significantly different from the two adult birth clusters, but overlapped with the two clusters of adults (Fig. 1). In all three years for which data were sufficient for analysis, the timing of births of primigravid females (Fig. 1d) was significantly different from both of the adult peaks ($p < 0.01$ for all; Table 2).

Most adult female *M. minimus* captured were either pregnant, lactating, or both (e.g., Fig. 2a showing data from 1982 and 1983). Births were significantly clustered in two broad peaks per year (Fig. 2c), one centered on March and the other, approximately six months later, on August/September (Table 2). The presence of large numbers of females that were both pregnant and lactating indicates that many (and perhaps almost all) females gave birth twice in each year. In all but one of the years for which data were sufficient for analysis, clusters in both periods were highly statistically significant (Table 2). There was no significant clustering of births between June 1991 and July 1992 (Table 2), despite collection of large samples in those years. There were no significant differences in timing across years.

For primigravid female *M. minimus* (Fig. 2b & 2d), there were two significant clusters of births, one centered in April and May and the other in August and September (Table 2). Births from primigravid females were also seasonal, as each of these clusters was statistically significant in every year in which enough data were collected for analysis, except for 1987, in which p was 0.06 (Table 2).

There were no significant differences in the timing of births of young females among years. In only one of seven comparisons, the first half of 1983, was the timing of adult and young females significantly different ($p < 0.05$).

Almost every adult female *E. spelaea* captured was pregnant, lactating, or both (Fig. 3a). Births in 1982 and 1983 were not significantly clustered, but the sample sizes were relatively small. Because the sample size was very small for *E. spelaea* in every year except 1991–1992, and because differences among years were small for other species, data from 1981 through 1987 were combined (Fig. 3c) for further analysis. In the combined data set and in 1991–1992 there were two significant clusters, one centered on March and another centered on August (Fig. 3c). In 1991, the August cluster was significant only if lactating females were included in the analysis. Many adult females were both lactating and pregnant (Fig. 3a), indicating that adults often produce two young in each year.

Four of 20 free-flying young female *E. spelaea* captured between 1981 and 1987 were pregnant (Fig. 3b). Births were in April, May, and July (Fig. 3d), but clustering in this small sample of primigravid females was not significant ($p > 0.10$).

The means of clusters of births were very similar in all three species. The only significant differences among these species were slightly earlier births in *M. minimus* and *E. spelaea* than *R. amplexicaudatus* in the March/April cluster in 1983 ($p < 0.05$ for both comparisons), and slightly later births in *M. minimus* than *R. amplexicaudatus* in the August/September cluster in 1982 ($p < 0.05$). A comparison of the periods that include 90% of all births for each species suggests that the degree of synchrony of

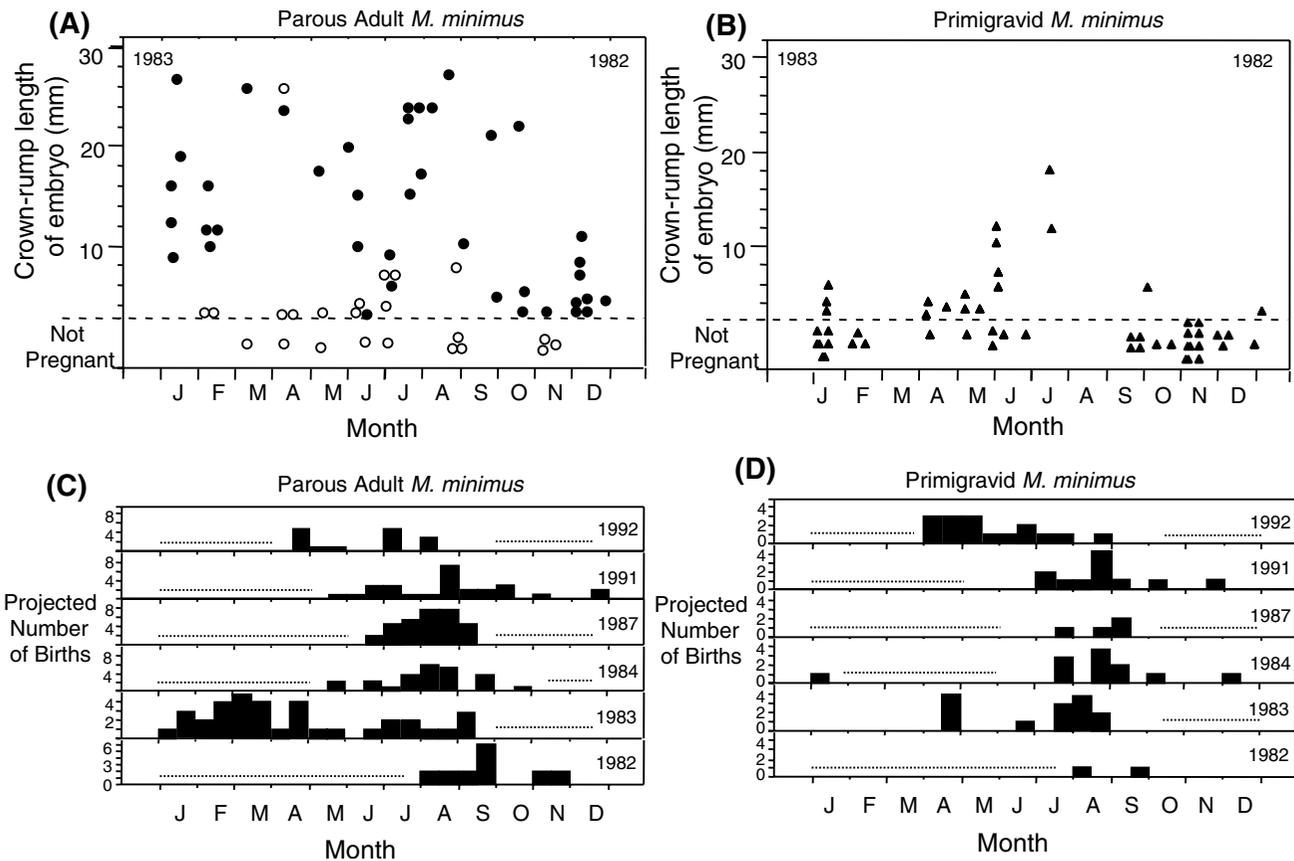


Figure 2
Reproductive status of *Macroglossus minimus*. (a) Sample data showing parous adult females from June 1982 to July 1983 (these months have been rearranged to display January to December for consistency with other figures). (b) Primigravid females from June 1982 to July 1983 (these months have been rearranged to display January to December). (c) Estimated timing of births in parous adults collected from 1982 to 1992. (d) Estimated timing of births in primigravid females collected from 1982 to 1992. Dashed lines indicate no data available. In (a), open circles indicate individuals lactating, and solid circles indicate individuals not lactating. In (b), triangles indicate individuals. Dashed lines in (c) and (d) indicate no data available.

reproduction was highest in *R. amplexicaudatus*, intermediate in *E. spelaea*, and lowest in *M. minimus* (Fig. 4).

Discussion

Seasonality and Synchrony

Estimated births were significantly synchronous and seasonal within and among all three species. This was the case even for the species in which pregnant or lactating females can be found in any month. Births of all three species were significantly clustered in most years, and births of multiparous females occurred in two peaks in the year, having a pattern of seasonal bimodal polyestry [15]. In all three species, the capture of many females that were simultaneously lactating and in the early stages of preg-

nancy indicates that many, and probably most, females produce young twice in each year. For *R. amplexicaudatus*, synchrony and seasonality could be inferred by visual analysis of the data, even without formal statistical analysis (Fig. 1). For *M. minimus* and *E. spelaea*, however, clustering was inconspicuous in the raw data (Figs. 2 & 3). For these two species, statistical analysis was necessary. Our results indicate that *M. minimus* and *E. spelaea* have a pattern that, by adding a subcategory to Happold and Happold's [15] nomenclature, could be described as extended seasonal bimodal polyestry, possibly with a post-partum estrus following one of the two periods of births. In contrast, *R. amplexicaudatus* has a pattern of

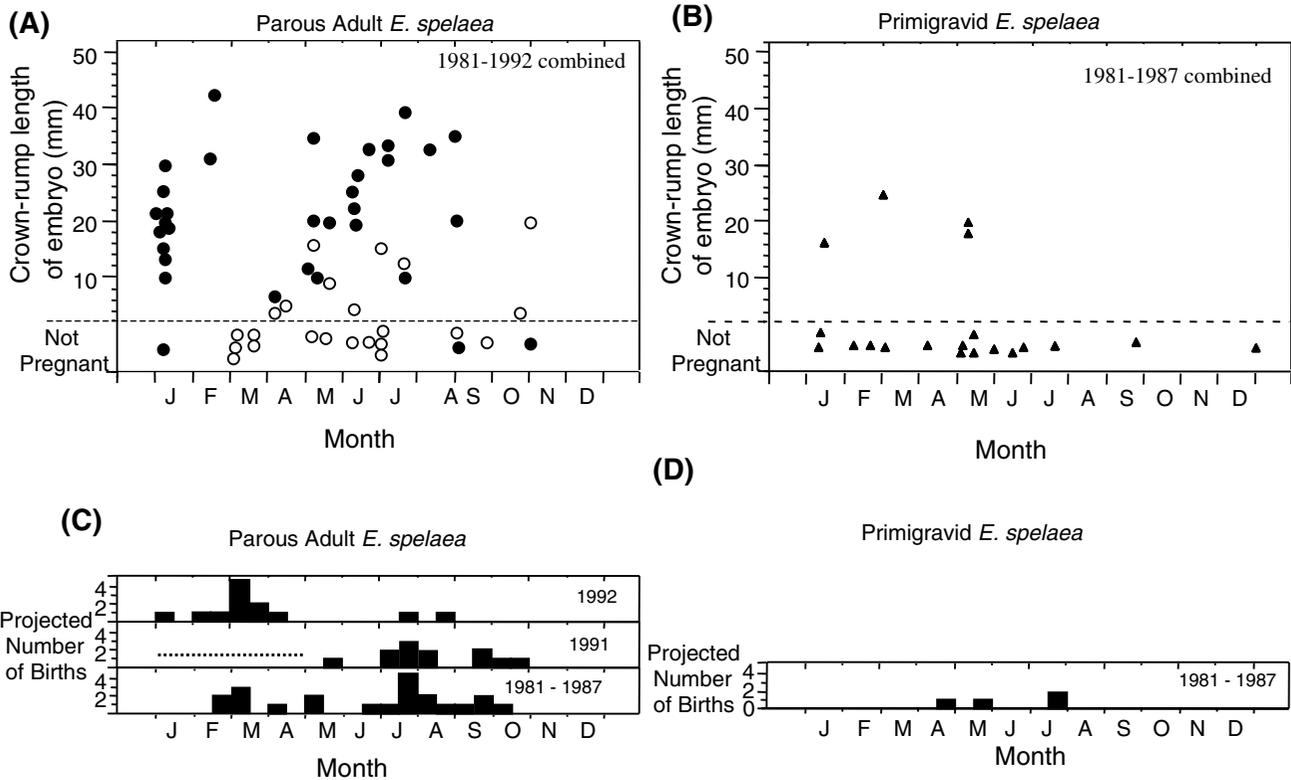


Figure 3
Reproductive status of *Eonycteris spelaea*. (a) Data from all parous adult females captured from 1981 through 1992. (b) Data from primigravid females from June 1981 through 1992. (c) Estimated timing of births in parous adults collected from 1981 to 1992. (d) Estimated timing of births in primigravid females collected from 1981 to 1987. In (a), open circles indicate individuals lactating, and solid circles indicate individuals not lactating. In (b), triangles indicate individuals. Dashed lines in (c) and (d) indicate no data available.

seasonal bimodal polyestry (following [15]), with a period of postpartum estrus following the March births.

Age-Specific Variation in Reproductive Timing

The data suggest that females of all three species usually become pregnant in their first year of life. In primigravid *M. minimus* and *E. spelaea*, the timing of births was not significantly different from that of adults. The one exception was a birth peak for primigravid *M. minimus* in 1983. For these two species, our data did not indicate whether young females typically have only a single pregnancy or two pregnancies in their first year. In contrast, the timing of births for primigravid *R. amplexicaudatus* differed significantly from that of adults, with primigravid young *R. amplexicaudatus* producing only a single young in their

first year, with births falling between the two peaks in births of adults.

Young *R. amplexicaudatus* appear to follow a conservative reproductive strategy in their first year, which may maximize their chance to produce at least one offspring, while minimizing their total reproductive costs. The production of their single young falls within the late dry season, and late pregnancy and lactation coincided with the end of the dry-season peak in flowering and beginning of any subsequent increase in fruiting in 1982–1983. As parous adults, female *R. amplexicaudatus* switch to a potentially riskier strategy that requires greater investment, but may result in higher reproductive output, by producing two young in each year. Their production of two young bracketing the

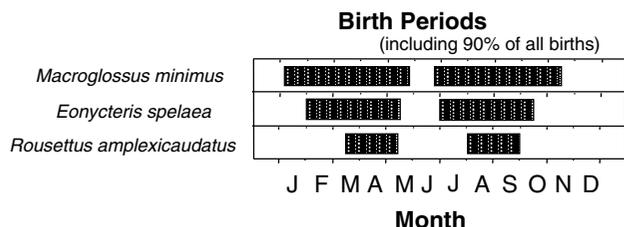


Figure 4
Estimated birth periods in three species of nectarivorous bats. Birth periods have been defined as the periods that include 90% of all births.

dry season and early wet season places greater total energetic and nutritional demands on these parous adult females. In addition, these two reproductive bouts may be more stressful on females or their offspring [14], as much greater portions of the highly demanding periods of late pregnancy, lactation, and weaning will generally fall outside of flowering peaks. Inexperienced young females may maximize lifetime fitness by minimizing energetic demands and risks to survival during their first reproductive attempt, while more experienced older females increase reproductive success by higher investment in offspring and with higher risks to themselves [9,14]. The data are also consistent with an alternative hypothesis, that young female *R. amplexicaudatus* have developmental constraints that prevent reproductive maturation and pregnancy at the younger age that would be required for synchrony with adults. Differences in reproductive timing between primigravid young females and parous adult females have been reported for several other species of Pteropodids [9,14,16].

Reproductive Strategies and Food Availability

All three species have two annual peaks in reproduction, with the first centered on March or April, at the beginning of the dry season, and the second centered on or near August, in the early wet season. These periods had higher flower and/or fruit abundance in 1982–1984 [17] and in 1991–1992 [18]. On Negros, most individuals of all three species are either reproductively quiescent or in early pregnancy in December and January, months of the late wet season when both flowering and fruiting were at their minima in 1982–1983 [17]. The general pattern of births in dry season and early wet season is also followed by frugivorous bats at this site [9,16], and by many other tropical bat species [1,15,19–21]. Frugivores at some sites tend to give birth only in the late dry season or wet season [22–

24]. Lim Boo Liat [25] reported that *E. spelaea*, *M. minimus*, and *R. amplexicaudatus*, along with frugivorous Pteropodid bats sampled in a Malaysian bat community, all produced young primarily in the months of February to June, months in which flowers were stated to be more abundant.

The three species all had significant synchrony of births, but differed in the breadth of the periods within which most births occurred (Fig. 4). These differences in breadth of birth peaks are correlated with differences in the diet resource peaks in these species. *Macroglossus minimus* is a specialist feeder in Malaysia [26,27], with species of *Musa* forming a major component of its diet in Malaysia and Indonesia [28]. On Negros, *M. minimus* is strongly associated with species of *Musa* wherever they are abundant [29,30]. Groves of domestic banana and abaca are abundant in agricultural areas on Negros and had been planted in some clearings at the forested sites. Additional species of *Musa* occur naturally in disturbed areas at the forested sites. These species flower relatively asynchronously and aseasonally, and each plant flowers for one to several months, providing over that time a steady supply of nectar and, except for domestic bananas, pollen. While all three bat species will feed upon species of *Musa*, *M. minimus* may have a competitive advantage in access to flowers of *Musa* sp. because *M. minimus* commonly roost under dead leaves in or near patches of *Musa*, while the other two species must travel long distances from cave roosts to reach most such patches. Thus, *M. minimus* may be buffered from strong seasonal changes in food abundance, permitting broad peaks in births, with relatively little selection pressure for highly synchronized periods of birth. Because *M. minimus* is a solitary species [26] (and personal observation), selective pressure for synchrony due to advantages of group living, such as huddling of young to reduce energetic demands, is unlikely.

Eonycteris spelaea is a generalist nectarivore that often commutes over distances of tens of kilometers to feed [26,27]. The species is known to feed on the flowers of a large number of different species of plants [27,31]. While *E. spelaea* includes species of *Musa* in its diet, *E. spelaea* lacks the strong association present between *M. minimus* and *Musa*. While *E. spelaea* feeds on many different plant species, it is possible that their diet varies seasonally in either food availability or in nutritional quality. If so, then more seasonal food sources for *E. spelaea* may favor the narrower peaks of births in *E. spelaea* than occurs in *M. minimus*. Alternatively, narrower birth peaks in *E. spelaea*, relative to *M. minimus*, may occur because tight synchrony of reproduction reduces losses to predators (e.g., snakes living in caves) through predator satiation or because tight synchrony of reproduction offers energetic benefits from huddling.

Rousettus amplexicaudatus is a nectar and pollen feeder [31], and on Negros also feeds heavily upon soft ripe fruit, especially in orchards (e.g., chico, guava, mango [32,33]). The first period of births in this species begins just before the peak of flowering during the dry season, and the second occurs in the early wet season, when many soft fruits produced from dry season flowers are ripening. The seasonal availability of these resources may favor the relatively high degree of synchrony in *R. amplexicaudatus*. Both *E. spelaea* and *R. amplexicaudatus* roost in large colonies in caves, and the energetic benefits of huddling of juvenile bats, or of predator satiation, may favor increased reproductive synchrony as well.

Variation in Reproductive Timing Among Years

In each of the three species, the timing of reproduction was similar across years, even in the severe drought in the el Niño year of 1983 [34,35]. The midpoints of birth peaks varied by only two weeks among years for parous adult *R. amplexicaudatus*, and by only one month for primigravid young. The fact that several of the differences were statistically significant for adults suggests that there may be some slight plasticity of timing in this species. However, the small magnitude of the differences indicates that reproduction in *R. amplexicaudatus* is timed very precisely, with relatively little variation among these years. In terms of biological relevance, this suggests that *R. amplexicaudatus* is sharply limited in the ability to adjust reproductive timing even in years that vary dramatically in weather and resources, and suggests that this species has little plasticity of reproductive timing [36]. In contrast, in three species of frugivorous bats on southern Negros, births were three to seven weeks earlier in the el Niño year of 1983 than in other years [9]. Two of these three species are known to have delays in embryonic development [14,35], suggesting that delayed development may facilitate adjustments in reproductive timing in particular years.

In neither of the other two species were differences in the timing of births among years significant. It is possible that we might have missed small differences that were not detectable because of low sample sizes for *E. spelaea* and because of high variance in the timing of births in *M. minimus*. Our data suggest that any such differences in timing, if they exist, are probably on the order of one month or less among these years. Differences in timing among years are smaller than differences reported for three frugivore species [9]. These nectarivorous bats may be less variable in timing because peaks in flowering may be more predictable from year to year, while fruit crops of some species are more likely to fail on Negros in drought years [17]. Because the timing of wet and dry seasons varied by two months or more among the years of the study [17,34] while the midpoints of birth seasons varied only by a few weeks, it may be that none of these species can make more

than minor adjustments in the timing of births to match differences in rainfall among years. Reproductive timing has been reported to be very similar among years in most other studies that have made these comparisons [37-39].

Adaptation to Climatic Seasonality

The timing of wet and dry seasons was quite variable on southern Negros [40], and the timing and amplitude of peaks of flowering and fruiting on southern Negros might be variable across years as well [17]. Variation across years would produce variable selection, in which different periods may be optimal for reproduction in different years. If so, there may be no selective advantage to tightly synchronized reproduction for some species, even if highly seasonal reproduction was favored in every single year. Instead, the average effects of selection might favor reproduction within broad temporal windows, producing the broad peaks in births seen in species such as *M. minimus*. Under these conditions, social species such as *R. amplexicaudatus* that roost in large groups might have evolved more tightly synchronized reproduction due to other selective forces, such as thermoregulatory benefits from huddling or satiation of predators when young become independent. Synchrony and seasonality are not necessarily favored by the same selective pressures.

These species are not necessarily well adapted to seasonal patterns on southeastern Negros. Seasonal patterns of rainfall can vary dramatically over short distances in the Philippines, and there is considerable variation in the timing and severity of wet and dry seasons, even among nearby sites on single islands [34]. On Negros, the eastern and western sides of the island, at sites less than 50 km apart, differ strongly in the severity of the wet and dry seasons, and also differ in the exact timing of rainfall [34,41]. Nearby islands differ by as much as several months in the average timing of wet and dry seasons [34,42]. However, the small amount of data available suggests that all three species of nectarivores appear to have similar patterns of reproductive timing on other islands [40]. If gene flow among populations is relatively high, it might negate the effects of selective forces favoring reproduction synchronized to seasonal events at any particular location. Both *E. spelaea* and *R. amplexicaudatus* can fly tens of kilometers nightly and will cross water barriers as well as agricultural land [27,29,43]. For these species, in particular, we predict that natural selection would favor periods of births that were centered on times that are best, on average, over an entire island or many islands. As a result, reproductive timing may or may not approach optimal timing for these species on southeastern Negros or any specific site. Species that move only short distances or populations that are relatively isolated may be more likely to evolve reproductive timing to match local differences in seasonal conditions. For example, one small frugivorous Philippine bat,

Haplonycteris fischeri, differs in reproductive timing by several months among islands only tens of kilometers apart [16]. This species apparently travels only short distances and rarely ventures out of forest [29], suggesting that gene flow among islands is low, which may allow different patterns of timing to evolve even among populations on nearby islands. In studies on New World frugivores that have compared sites that are relatively near each other, both the reproductive patterns and the timing of wet and dry seasons have been similar among sites, suggesting that selection pressures on seasonality are also similar [19,44,45]. In contrast, reproductive timing often varies between sites separated by large distances such as the hundreds of kilometers between sites along large latitudinal gradients [reviewed by [1]].

Potential Advantages and Limitations of the Resampling Analysis

Resampling methods with circular statistics was chosen for these analyses because the expected distributions of birth dates and capture dates for non-reproductive females were not predictable due to uneven sampling among months [see [10,12]]. Parametric methods for analyses of timing of birth have used data in the form of direct observations of birth [39,46-49], but direct observation of births or neonates is often impractical. We suggest that the adaptation of resampling statistics is better than previous approaches to analysis of data sets with these problems because it allowed statistical testing using all data from all females, whether reproductive or non-reproductive. However, this approach has some statistical problems, and methods that solve some of these problems may be feasible. The three major statistical problems in this study arise from the treatment of multimodal distributions, from 'observations' that are themselves predictions (birth dates predicted from embryo size), and from differences among years in sampling periods that caused censoring of data. First, bimodal distributions of births require decisions about the time point chosen as the boundary between the two parts of the year analyzed for each of the two birth periods. The choice cannot be made a priori, and thus may be biased. In our analyses, we were able to assess how sensitive the results were to the choice of boundary times between birth peaks. In these cases, the analyses gave similar results when boundary dates ± 1 month were tested. However, we know of no method to make the choice of boundary dates in a statistically unbiased manner. Second, birth dates predicted from conceptus diameter have two sources of statistical error, the error in estimate of conceptus diameter and the error in the estimate of birth date. These two sources of error may be inappropriately combined in our model. If both sources of error are unbiased, this should tend to obscure clustering, reducing the probability of detecting clustering or of detecting differences among years or species. Third,

'censored' data due to a lack of samples at some times caused us to discard data from some months when we were comparing either two different species or two different years in order to match the sampling periods. Because the results were robust to differences in cut-off dates, and because the other sources of error would reduce the power to detect differences, these problems were judged acceptable. Additional development of these techniques might reduce any effects of these problems.

Results of these analyses were most robust when the data were not censored by periods in which there were no captures. To test for possible effects of periods with few or no data, data sets from both nectarivores (this paper) and frugivores [9] were tested and then retested after censoring of parts of the data. The resulting analyses gave similar results despite the censoring if captures of females were distributed evenly through the period of interest (usually a year) for both large data sets (100 or more females) and small data sets (10 females, of which about half were pregnant) (Heideman, unpublished data). However, when data were available from only part of the period of interest, we observed effects due to the loss of data. First, type II error in the detection of synchrony was increased (failure to detect synchrony when it occurs). In addition, when using censored data there was systematic bias in estimates of the mean date of clusters of births. For example, data collected at the end of a period of reproductive quiescence and the beginning of the period when females become pregnant would advance the estimate of the mean birth date, because females that conceive late will not be present in the sample. Sampling only near the end of gestation and the subsequent months would cause the opposite shift, because females that give birth early in the peak will not be represented. For these reasons, in this study we limited our analysis to periods of data collection of at least four months, and we did not assess data from sampling periods in which we had reason to suspect that the timing of data collection had the potential to create systematic bias.

Consistent with our observations, reviews of the use of resampling methods in ecology [10,12] suggest caution in the development of tests and concern for potential biases. Statistical problems exist for all of the methods – nonparametric, parametric, or resampling – that have been used to analyze seasonality of reproduction in mammals. We suggest that the applications of resampling techniques used here are a valuable improvement over the existing statistical approaches to assessing seasonality and synchrony in many field studies.

Conclusions

Three species of nectar feeding Pteropodid bats on southeastern Negros Island have a highly seasonal pattern of

reproduction, with all of the species having two birth peaks. However, these three species differ in the breadth of birth peaks, and the breadth of peaks appears to match the degree of synchrony in their food sources. The relative lack of variation in reproductive timing among years suggests that there is little phenotypic plasticity in reproductive timing, and that these species use seasonal cues of some kind [36] to regulate reproductive timing. The resampling methods used were able to distinguish small differences of weeks in the timing of births among years or species. This suggests that resampling methods will be useful statistical methods for these kinds of data sets.

Methods

Study Sites

Data were obtained from two different year-long periods (1982–1983, 1991–1992) and during one to four months in three other years (1981, 1984, 1987) on southeastern Negros Island in the Central Philippines.

Samples of bats were obtained at three sites on Negros Island, all within 17 km of each other. One site (Balinsasayao) was primary lowland rain forest with montane elements, mixed with small patches of agriculture and second growth (Lake Balinsasayao; sampling centered on 9°22'N, 123°9'E, elevation 830 – 1200 m); a second (Talinis) was on an elevation gradient with mixed agricultural land, second-growth forest, and primary lowland forest grading into montane and mossy forest at higher elevations (Mt. Talinis; sampling centered on 9°16'N, 123°13'E; elevation 450 – 1400 m); and the third (Orchard) was an urban orchard at sea level within the city limits of Dumaguete City (Ausejo Farm; 9°19'N, 123°18'E; elevation 5 – 15 m). Reproductive data from all three sites were combined because we consider all three sites to sample a single population of each species. Two of the species we studied, *Eonycteris spelaea* and *Rousettus amplexicaudatus*, are known to forage over distances over 20 km [27,29], greater than the 17 km between the study sites. The third species, *Macroglossus minimus*, typically forages shorter distances of up to 2.5 km [26,29], but individuals could readily disperse over distances greater than 17 km in a single night.

Brief descriptions of the habitats are provided here; more detailed descriptions of two of these study sites have been provided elsewhere [17,18,29,50,51]. The vegetation at the Orchard site was dominated by common orchard fruits, including coconut (*Cocos nucifera*), chico (*Achras sapota*), mango (*Mangifera indica*), guava (*Psidium guajava*), and banana (*Musa* spp.), but with many other flowering species nearby, including flowering species known to be used by bats such as abaca (*Musa textilis*) and kapok (*Ceiba pentandra*). The most common bat captured in the

orchards was *R. amplexicaudatus*, presumably because this species most commonly includes soft fruits in their diets.

The two higher-elevation sites were largely lowland dipterocarp rain forest, with the higher elevations grading into oak/laurel montane and mossy forest. The highest elevations had some elements of mossy forest. At the Balinsasayao site at 800–1000 m elevation, where most sampling was concentrated, the forest canopy was typically 15–30 m high, with emergent trees reaching to 60 m high. The dominant tree species were in the Dipterocarpaceae, Myrtaceae, and Lauraceae [52], with approximately 20 species in the Moraceae (mostly species of *Ficus*) growing as vines, shrubs, and free or strangling subcanopy, canopy, or emergent trees [18,52]. Approximately 25% of the two higher-elevation sites consisted of clearings, most of 0.5 – 2 ha, being used for subsistence agriculture. Approximately one-half of the clearings held abaca (*Musa textilis*), and many held wild species of *Musa*.

The Talinis site [18] was a mosaic of agricultural land and secondary forest at its lower elevations, and primary forest at higher elevations. Fifty percent of plants sampled at the lower elevations were, in order of abundance, coconut, domestic banana, and coffee. The most common non-cultivated woody plants in this area were a shrub, *Melastoma* sp. (Melastomataceae), and a tree, *Ficus septica* (Moraceae). In the primary forest at the Talinis site, abundant tree, shrub, and vine species were generally similar to those at Balinsasayao. The most speciose family at the Talinis site was Moraceae, with 16 species identified [18].

Rainfall and temperature records were collected at the Balinsasayao forest site on Negros [34] and at the Talinis site [18], and were obtained from the Philippine National Weather Bureau (PAGASA) for the Orchard site [41,42]. The range of mean low and mean high temperatures was 18 – 25 °C at the Lake Balinsasayao site, 14 – 28 °C at the Talinis sites, and 24 – 31 °C at the Orchard site, with seasonal variation in mean monthly high or low temperature of only about 3 °C at any given site. Due to the effects of its higher elevation, the Balinsasayao site received about 2–3 times more rainfall (3100 mm/yr) than the Orchard site (1200 mm/yr) [34]. Rainfall was mildly seasonal at all three sites, with the driest months (usually March, April, and May) each receiving only about 1/4 to 1/2 of the average monthly rainfall of the wettest months [34]. In the years of the study, 1983 and 1992 had unusually severe dry seasons with almost no rain (average of less than 5 mm/month near the Orchard site, but 10–40 mm at Balinsasayao). In the severe el Niño of 1983, the dry season started in January, two months earlier than the average start of the dry season.

At the Balinsasayao site, there was variation in flower and fruit abundance [17] that corresponded to seasonal changes in rainfall. Flowering peaked in the dry season (March to May) and early wet season (June – September), with about a two- to four-fold increase in flower abundance over the late wet season (October-December). There were increases in fruiting in the early wet season, but these seasonal changes in fruiting were generally statistically insignificant. The data indicate that there can be substantial differences in the phenology of flowering and fruiting from year to year [17]. At the Talinis site in 1991–1992, the timing of flowering and fruiting at the community level [18] was similar to the timing of fruiting and flowering at Balinsasayao in 1982–1984 [17]. The number of plants in flower and the abundance of flowers peaked in May and June in 1991, with another small peak in the number of plants in flower in July and August, and in 1992 a large peak in March, April and May of 1992 [18]. The number of plants in fruit peaked in July and August of 1991, but total fruit abundance was highest in May and June of 1991 and in March and April of 1992. These data suggest that the general pattern on southeastern Negros is for peaks in flowering in the dry season and early wet season, and of fruiting in the late dry season and early wet season, with some variability among years.

Study Animals

The three species discussed in this study are primarily nectarivorous and are ecologically important pollinators through much of Southeast Asia [27,28,53]. All three species have morphological specializations for nectar/pollen feeding, including an elongated rostrum with small teeth and an extremely long tongue with bristles that can capture nectar and pollen. Two of the species, *E. spelaea* and *M. minimus*, feed mostly on nectar and pollen [31]. In Malaysia, species of *Macroglossus* are diet specialists, while *E. spelaea* is a generalist feeding on over 31 plant species [27]. *R. amplexicaudatus* probably feeds frequently on soft fruit as well as nectar and pollen; the relative proportions of their diet formed by fruit, nectar, and pollen are not known [31]. All three species were positively associated with a measure of flowering on Southeastern Negros [18]. These three bat species comprise, along with a rare fourth species (*Eonycteris major*; 0.5% of captures of nectarivorous bats) the nectar- and pollen-feeding guild of fruit bats on Negros Island. Other species of Pteropodids on the island feed occasionally on nectar and pollen as well, but rely more heavily on fruit [32,51,54].

Data were obtained from 374 adult female and 299 young female *R. amplexicaudatus*, from 185 adult female and 169 young female *M. minimus*, and from 56 adult female and 20 young female *E. spelaea*. The data recorded from captured bats included identification number (tattoo, band number on collar, or catalog number), forearm length,

body weight, sex, age (neonate, juvenile, subadult, young adult, or adult), and reproductive status (length of palpated/measured embryo, teat size, lactational status, and degree of development of mammary tissue). Embryo size was measured as the greatest length of the conceptus along with the surrounding uterine tissue; this is slightly larger, by about 1 – 2 mm, than the crown-rump length of an embryo (Heideman, unpublished data). Voucher specimens were deposited in The University of Michigan Museum of Zoology and at the National Museum of Natural History.

Approximately 60% of the 1103 observations were made on females that were marked and released. For these females, the presence and size of embryos were estimated by palpation of the abdomen. The accuracy of these estimates was tested by palpation of the 40% of females captured that were then euthanized for reproductive necropsy. Error rates were very similar for each species, and so only the combined data for all three species are presented. The overall rate of false positives or false negatives for detection of pregnancy was 6% (11 errors in tests of 198 euthanized bats, of which 153 were pregnant and 45 were not pregnant). Nine of the errors involved the smallest embryos (9 misdiagnosed females of 138 females with embryos < 4 mm or not pregnant). Misdiagnosed pregnancies were distributed relatively evenly throughout the year. The average error in the size estimates of embryos from palpation of females that held embryos was ± 2 mm ($n = 153$ embryos). Because almost all bats captured in 1991 and 1992 were released, and therefore error checking of data on small embryos was not possible, for those years we did not include data from females with putative small embryos (< 6 mm), for which we judged our error rate to be highest. Only data from first captures were used in this analysis.

Separate analyses were conducted on parous adult females and primigravid females, because the two age classes can differ in the timing of reproduction. Females were defined as multiparous adults if they had fused phalangeal epiphyses [55] and large teats [16]. Females were defined as primigravid if they were pregnant and had unfused phalangeal epiphyses and/or small teats, and nulliparous if they were not pregnant and had unfused phalangeal epiphyses and/or small teats. During the last 1/2 – 1/3 of pregnancy, it was difficult to distinguish between primigravid and multiparous females of all three species because the epiphyses were usually becoming fused and the hormonal events associated with late pregnancy were causing final development and growth of the teats. Therefore, it is likely that some primigravid females in the second half of pregnancy were incorrectly classed as multiparous adults; this source of error would have reduced the probability of detection of differences in timing

between primigravid and multiparous adults. In 1991 and 1992, this difficulty was reduced, after it was observed that the teats of females that have suckled have a greatly broadened tip, creating a teat with a narrow neck flaring to a broader tip.

Data Analysis

All birth dates were estimated using approximations of the daily embryonic growth (maximum diameter of the conceptus at birth divided by an estimate of the duration, in days, of gestation from first macroscopic appearance of the conceptus as a palpable uterine swelling of 2–4 mm to birth; Table 1). In addition, it was assumed that approximately 10 days were required for an embryo to become both macroscopically apparent and palpable. For *R. amplexicaudatus*, a test of the estimator using a stepwise regression analysis of conceptus diameter on date indicated that this estimator explained 87% of the variation ($R^2 = 0.87$; $p < 0.05$).

For the data analysis, synchrony was defined as the clustering of births within a year, and seasonality was defined as the tendency for clusters of births to fall at approximately the same point in each of two or more years. Seasonality and synchrony of births were assessed using circular statistics [13] with significance at $p < 0.05$. The year was considered as a circle, with each of the 365 days of the year a point on the circle, beginning with the morning of 1 January at 0° ; for example, 1 July falls at approximately 180° , and 1 October at approximately 270° . Circular statistical methods make use of measures equivalent to or analogous to the mean and variance. In circular statistics, the estimate of central tendency is the mean angle; the variance around that mean is the angular variance [13]. Equations 1.3.7 from [13] were used to calculate the mean rectangular components of a vector

$$\bar{x} = \frac{1}{n} \sum_{i=1}^n \cos \phi_i \quad \text{and} \quad \bar{y} = \frac{1}{n} \sum_{i=1}^n \sin \phi_i \quad \text{where } \phi_i \text{ were}$$

the dates in radians of births from a data set. The length of the mean vector was calculated from equation 1.3.8 from [13], $r = (\bar{x}^2 + \bar{y}^2)^{1/2}$. The mean angle was calculated using equation 1.3.9 from [13] $\bar{\phi} = \arctan(\bar{y} / \bar{x})$ if $\bar{x} > 0$ or $\bar{\phi} = 180^\circ + \arctan(\bar{y} / \bar{x})$ if $\bar{x} < 0$. The value for the mean angle will be indeterminate if $\bar{x} = 0$ and $\bar{y} = 0$, but this case never occurred for our data. The angular variance was calculated using equation 2.3.1 from [13], $s^2 = 2(1 - r)$, which is "... asymptotically equivalent to the variance in linear statistics" [13]. The statistical significance of synchrony and seasonality was assessed using randomization techniques [10-12]. The null hypothesis for tests of synchrony was that births were distributed randomly through the entire year. Births were considered to be seasonal if

there was significant clustering of births, as measured by the angular variance, and similar mean angle in each year of sampling.

Two randomization algorithms were developed to test aspects of synchrony and seasonality. Code in Symantec Think C++ for Macintosh v. 7.0 is available from PDH for both algorithms. The first of the two algorithms tested for significant clustering of births. It used the angular variance [13] of birth dates in a data set as a measure of clustering, with lower angular variance indicating greater clustering. The algorithm compared the angular variance of the original data set to the angular variance of 10,000 iterations of data points randomly reassigned to capture dates (without replacement). Clustering of births was considered statistically significant if the angular variance was lower in the original data than in 95% of the randomized iterations.

A second algorithm compared the timing of births in different years or between species. First, the difference between the mean angles of birth date (equivalent to mean birth date [13]) was obtained for the two years or two species being compared. Then, in each iteration of the randomization procedure, each data point was randomly reassigned to one of the two the two data sets in a process of random selection without replacement. In each iteration, the difference between the mean angles of the randomized data sets was obtained and compared to the difference in mean angles of the original data sets. Differences in birth peaks were considered significant if the difference in mean angles of the two original data sets was larger than the difference in mean angles in randomized data from more than 95% of 10,000 iterations.

Data from particular years were compared only if samples were obtained in both years or both species over a similar range of months. Whenever sampling was incomplete in one data set under comparison, the data set that sampled more months was truncated to match the sampling period of the shorter data set. Failing to match the sampling periods could produce falsely significant differences in timing if, for example, only the beginning of a birth period was assessed in one year (thus missing late births), while only the end of a birth period was assessed in another (thus missing early births). Accurate characterization of the timing of birth periods requires data that sample the entire birth period, but differences between years can be assessed with less-complete data sets if they are matched for sampling period and effort.

In some species, there was evidence for two birth peaks in each year (e.g., females that were lactating to feed a dependent young and also were pregnant). An *ad hoc* method following Batschelet [13] was chosen to analyze

double peaks because there is no statistically unbiased method to identify and analyze double peaks within a year; data sets were divided at a point midway between potential peaks, and each half was analyzed separately.

Capture of lactating females indicates that birth must have occurred within the preceding few months. For the smaller data sets in the study (e.g., some for *E. spelaea*), lactational data were used to increase sample size, at cost of decreasing the accuracy and precision of the estimates. The analyses assumed that, on average, a lactating female would be captured at the midpoint of lactation; thus, parturition dates for lactating females were estimated by backdating the number of days equal to one half the duration of lactation (Table 1). Tests using lactational status are indicated in the results.

In order to test the robustness of the results (i.e., to test how sensitive the results were to particular choices for major input parameters), randomization tests were repeated over a range of embryonic growth rates and sizes at term ($\pm 10\%$ or more) and, for species with double peaks, a range of division points between peaks (± 2 months). The one case in which the results were not robust to variation in growth rate or division point is noted in the results.

Authors' contributions

PDH collected the data from 1981–1987, with assistance from RBU during the 1983, 1984, and 1987 data collection periods. RBU collected the data from 1991 and 1992. PDH developed the analytical methods and carried out the statistical analyses. PDH was the lead author in writing the manuscript, and RBU contributed some entire sections and contributed substantially to extensive revisions of the manuscript. Both authors read and approved the final manuscript.

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