The timing of reproduction in the fruit bat *Haplonycteris fischeri* (Pteropodidae): geographic variation and delayed development

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(With 8 figures in the text)

In climatically seasonal habitats, favourable periods for reproduction may be simply determined by large annual changes in temperature or rainfall. In contrast, in climatically less seasonal habitats, reproductive timing may be determined by a wide variety of seasonal factors. Three hypotheses regarding reproductive timing were tested for a fruit bat, *Haplonycteris fischeri* Lawrence, by comparing reproductive timing and climate at four moderately seasonal Philippine sites with differing climates. Bats were sampled in five years on Negros Island (9°22′ N, 123°11′E), and in one to four months on four other islands. Flower and fruit abundance was monitored in two years on Negros. In five years on Negros, parturition and lactation coincided with the time of the average dry-wet season transition and early wet season, but did not vary in response to substantial annual variation in the onset of rains. Reproductive timing did not change in response to annual variations in flower or fruit abundance; lactation coincided with a peak in fruit abundance in one year, but not in a second, and reproductive success appeared to be reduced when lactation coincided with scarce resources. At a second site with a different pattern of rainfall, reproduction was nevertheless synchronous with Negros. Samples from two of the three remaining localities indicate a two- to three-month lag in reproductive events relative to Negros, despite rainfall patterns remarkably similar to that of Negros. All three hypotheses for reproductive timing were rejected. As an alternative, *Haplonycteris* may evolve timing patterns in response to local seasonal patterns of resource abundance.

Haplonycteris has an eight-month post-implantation delay in embryonic development. Six hypotheses on the adaptive significance of this delay in *Haplonycteris* were evaluated. Three were rejected, but the data were consistent with the remaining hypotheses: (1) The delay sets the time of parturition at a particular time of year; (2) the delay allows all females to produce young relatively synchronously; and (3) the delay allows females to resorb or abort defective embryos without losing an opportunity for reproduction.

Contents

Introduction

Late pregnancy, lactation and weaning are the most demanding periods in the reproductive cycles of most mammals (Migula, 1969; Studier, Lysengen & O' Farrell, 1972; Millar, 1975, 1978, 1979; Wunder, 1985). Mammals may be able to increase their reproductive success by undergoing the stresses of late pregnancy, lactation and weaning during optimum periods (Bradbury & Vehrencamp, 1977; Bronson, 1985). Optimum periods are usually defined as periods of abundant or high-quality resources (Smith, 1974; Vaughan, 1978; Racey, 1982), but the optimum period for late pregnancy to weaning for an individual female may instead be at other times: when conspecifics are reproducing (e.g. if clustering of neonates is important for conservation of heat); when competitor populations are at low densities; when migratory competitors or predators are least abundant; or when climatic conditions are least harsh.

Considerable evidence from seasonal habitats supports the hypothesis that bats time reproduction to correspond to peaks in resource abundance (Heithaus, Fleming & Opler, 1975; Bradbury & Vehrencamp, 1977; Bonaccorso, 1979; Racey, 1982; Dinerstein, 1983); the evidence from less seasonal habitats is scanty. Resource peaks can be difficult to define and detect where strong seasonal change is lacking (e.g. Medway, 1972; Putz, 1979). In tropical rainforest habitats, resource peaks have often been inferred from annual patterns of rainfall and by assuming that biotic factors correlated with particular events in annual rainfall cycles at one location will have the same relationship elsewhere (Mutere, 1967; Fleming, Hooper & Wilson, 1972; Fayenuwo & Halstead, 1974). Such studies have often found correlations between reproductive timing and various climatic or resource variables. However, because we rarely know the precise diet and limiting resources of the species studied, the argument that reproductive timing is optimal lacks strength. A good alternative test is to examine a single species under a variety of conditions, contrasting a series of hypotheses on the timing of reproduction.

Animals attempting to time reproductive events to coincide with some optimum period face two problems: (1) prediction of optimum periods, and (2) constraints on their ability to respond to optimum periods or to the cues predictive of optimum periods. Accordingly, any examination of the causes of reproductive timing should consider the timing and predictability of optimum periods and the ability of an organism to respond to that variation.

In this paper, I discuss the reproductive timing of Fischer's pygmy fruit bat, *Haplonycteris fischeri* Lawrence, a strictly forest-dwelling, 18-g bat endemic to the Philippine archipelago. Although the species is apparently primarily frugivorous, the bats may also feed on flowers, and occasionally on leaves during part or all of the year (Utzurrum, 1985; Utzurrum & Heideman, unpubl. data).

Features of the reproductive cycle of *Haplonycteris* (described below and in more detail in Heideman, 1987) make it a particularly appropriate species for tests of hypotheses of reproductive timing. *Haplonycteris* adjust the timing of reproduction in such a way that females forgo the chance to produce a second young in each year, implying first, that reproductive timing is of great importance, and second, that seasonal variation might preclude successful reproduction during

some parts of the year. *Haplonycteris fischeri* are unusual in having a remarkable eight-month post-implantation delay in development, and in having only one young per year, although the relatively equable, only slightly seasonal environment would seem to permit more frequent reproduction. As a result, this small bat has the longest gestation known in bats, up to 11·5 months in parous females.

Hypotheses and predictions for timing of reproduction

First, the reproductive timing of *Haplonycteris* in a relatively aseasonal tropical rainforest habitat is described and then three hypotheses to account for particular patterns of reproductive timing, focusing on the effects of climate and its relation to resource abundance, are tested. The three hypotheses are: (1) the timing of wet and dry seasons determines the timing of reproduction; (2) reproduction is timed to avoid the part of the year when cyclones are most frequent; and (3) reproduction is timed to avoid periods when avian migrants or frugivores are abundant. Six hypotheses regarding the evolutionary significance of the manner in which *Haplonycteris* achieve their pattern of reproductive timing are also discussed.

If the timing of wet and dry seasons determines the timing of reproduction, then: (1) the timing of reproductive events in such conditions should be correlated with seasonal changes in rainfall; and (2) disjunct populations should reproduce at corresponding points in the annual climatic cycle.

Cyclones occur somewhat seasonally in the Philippines, with more than 75% occurring in the months of July–December (Thorp, 1962). The heavy winds and rain associated with cyclones may hinder or prevent foraging by fruit bats for several days (unpubl. data). Current evidence suggests that pteropodids generally have low protein diets, ingesting much more carbohydrate than required in order to obtain sufficient protein (Thomas, 1984). In addition, captive animals that do not eat become very weak and often die within 24 hours. Thus, it is quite possible that a single cyclone during late pregnancy or lactation, when protein requirements are high, would result in reproductive failure for a fruit bat like *Haplonycteris*. If reproduction is timed to avoid the cyclone season, *Haplonycteris* at all sites should time reproduction to avoid the months of July through December.

Because relatively few terrestrial non-volant vertebrate frugivores or predators occur on the oceanic islands of the Philippines, avian competitors and predators are likely to be more significant than elsewhere in the tropics. If the presence of migratory avian competitors or predators reduces reproductive success, then all populations are expected to undergo peaks in reproduction when migrants are absent, during the summer months of April–September.

Methods and materials

The major study site was the Lake Balinsasayao watershed in the mountains of southern Negros Island, located in the central Philippines (9°22′N, 123°11′E; 800–1100 m; Fig. 1). Samples of *Haplonycteris* were also obtained at 4 other sites (Fig. 1): the boundary region between Isabella and Cagayan provinces in northern Luzon (17°N, 122°E; 50–300 m), Biliran Island (11°32′N, 124°32′E; 670–920 m), central Leyte Island (10°46′N, 124°49′E; 500–650 m), and Bohol Island (9°42′N, 124°7′E; 300–400 m).

Haplonycteris is absent from a sixth island, Maripipi, only 9 km north of Biliran Island (Fig. 1), despite appropriate habitat. This suggests that even short water gaps may be barriers to gene flow, and that the bats on each island may reasonably be considered as distinct populations.
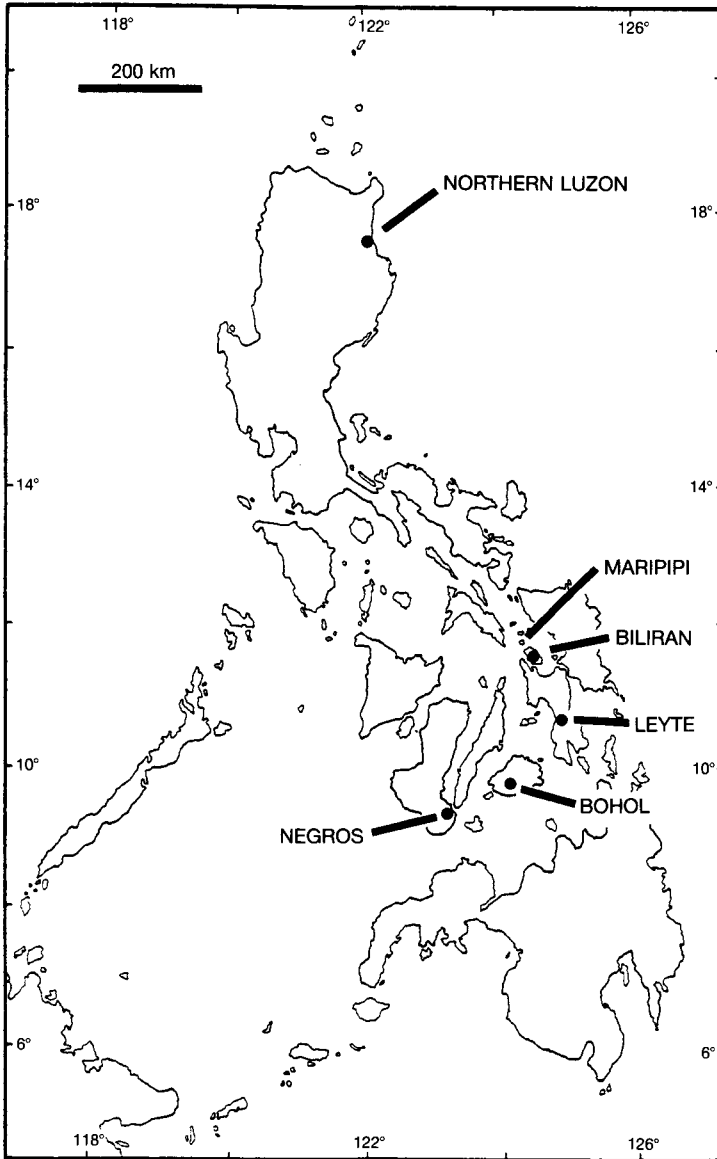
FIG. 1. The Philippine Islands: the study sites are marked with solid black circles.

All sites consisted of primary upland to submontane dipterocarp forest (Antone, 1983; Heideman, 1987). The elevational differences between sites are probably not significant, because those between most sites can easily be covered by a bat within a few minutes, and because the species ranges from near sea level to over 1500 m.

Approximately half of the 650 individuals captured at the Negros site were marked and released after external examination of reproductive condition, including palpation for embryos. Embryos were detectable by palpation if the diameter of the uterus at the conceptus was 3 mm or greater. The accuracy of palpation for

detecting small embryos was tested by comparing recorded results of palpations of live bats to autopsy results on the same bats following euthanasia. For the most difficult categories of females (those lacking embryos or with uterine swellings of 3 mm or less) over 95% were correctly categorized by palpation. Embryo size estimates for palpated embryos greater than 3 mm were within 20% of measured diameter 95% of the time. Autopsies were performed on all animals not released, and the reproductive tracts were preserved in Bouin's solution. Nipple size (tiny, small, medium or large), lactational status (not lactating, lactating clear fluid, lactating slightly cloudy fluid, or lactating white milk), and the degree of development of mammary tissue (not developed, slightly developed, moderately developed, or well developed) were recorded. Nipples were generally small until the last month of the first pregnancy, normally at age 11–12 months. The development of the joints of the phalanges in the wings of all animals was recorded (epiphyses visible or not visible, and joints 'swollen' or 'knobby'; Barbour & Davis, 1969). The phalangeal epiphyses were detectably separated until about age 8–10 months (unpubl. data). Age classes were assigned on the basis of wing-joint development, reproductive status and, for immature animals, weight. Animals with fused phalangeal epiphyses and 'knobby' joints were classed as adults; females that were pregnant, but had unfused epiphyses, swollen joints, and/or tiny nipples were classed as primigravid young adults; animals weighing more than 2/3 adult weight with unfused epiphyses and/or swollen joints were classed as subadults; immature animals weighing less than 2/3 but more than 1/3 adult weight were classed as juveniles; and immature animals weighing less than 1/3 adult weight were classed as neonates. Females were classed as parous if they had fused epiphyses, knobby joints, and medium or large nipples. Selected reproductive tracts were embedded in paraffin, serially sectioned at 5 to 10 microns, stained with haematoxylin and eosin, and examined by light microscopy.

Samples of bats from Negros were available from June 1979, June 1981, at monthly intervals from June 1982 through June 1983, February 1984, and at monthly intervals from April 1984 through July 1984. Samples of bats were obtained from northern Luzon in May, August, October and November of 1981; from Biliran Island in April 1984 and April 1987; from Leyte Island in May 1984 and March 1987; and from Bohol Island in June 1987.

Monthly climatic data were recorded at the study site on Negros during the 1982–83 field season; records at the site were continued by others during the following 12 months (Cadelina, unpubl. manuscript). Because monthly rainfall at the study site was highly correlated with rainfall 14 km east at Dumaguete City (Heideman, 1987), rainfall records obtained from the Dumaguete City Weather Station on Negros were also used to indicate long-term rainfall patterns. Rainfall records for the other sites were obtained locally, from the Philippine National Weather Bureau (PAGASA), and from published summaries for nearby sites (e.g. Manalo, 1956; Wernstedt, 1972).

The phenology of flowering and fruiting at the Negros site was determined from August 1982 through June 1983 and in April, June and July 1984. Those results will be presented elsewhere (and see Heideman, 1987), and only summaries of the methods and results will be presented here. In each month, all trees, vines, and shrubs within three 100×6 m plots and all of the canopy trees on 2 hillsides (approximately 1 ha each) were recording as flowering, fruiting, both, or non-reproductive, and approximate numbers and relative volume of flowers and fruits were estimated.

Results

Annual reproductive pattern

A detailed description of the annual reproductive cycle of *Haplonycteris* will be published elsewhere (unpubl. manuscript; and see Heideman, 1987); a summary will be presented here.

On Negros, parturition in multiparous females occurred in June in all five years of sampling (Fig. 2). Females were in lactation for about 2·5 months, and weaned their single offspring in late September and October (Fig. 3). Females had a post-partum oestrus and most were pregnant
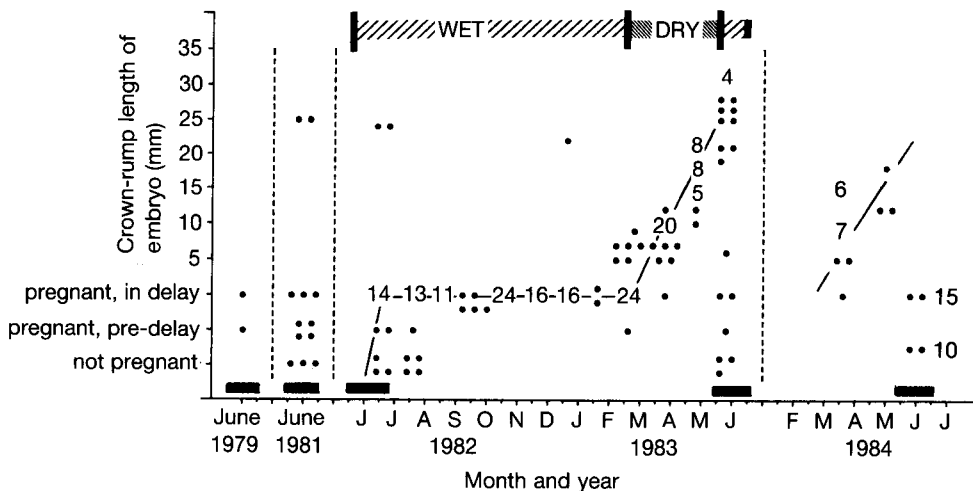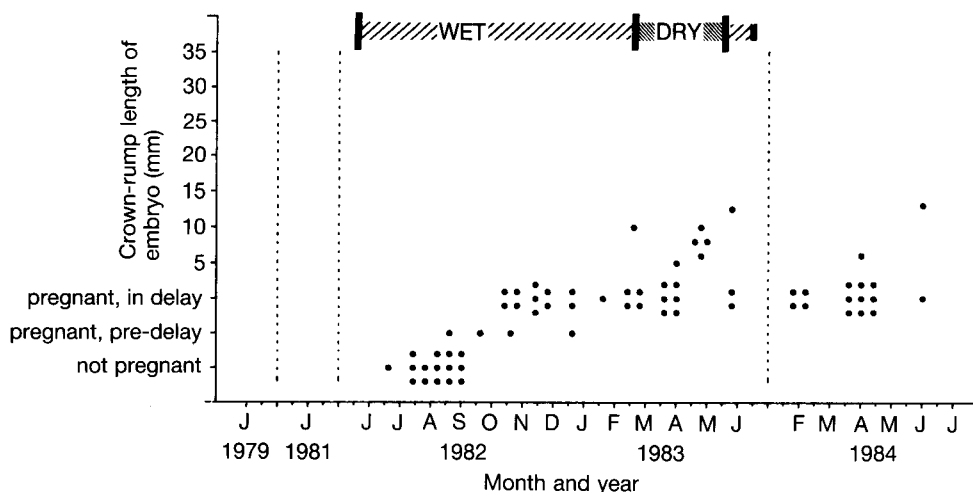
FIG. 2. Reproductive condition of multiparous female *Haplonycteris fischeri* from Lake Balinsasayao, Negros Island, from 1979–1984. The 'non-pregnant' and 'pregnant pre-delay' categories were clearly distinguishable only microscopically. Females captured from April–July, 1984, were examined alive and released; those lacking a detectable embryo from these months are represented midway between the two categories. The dots represent individual females, numbers represent that number of females falling at a single point, and the wide bars represent the approximate period of parturition in each year. The wet and dry seasons (defined arbitrarily as the nine wettest and three driest months of the year) are indicated with labelled bars at the top of the figure.
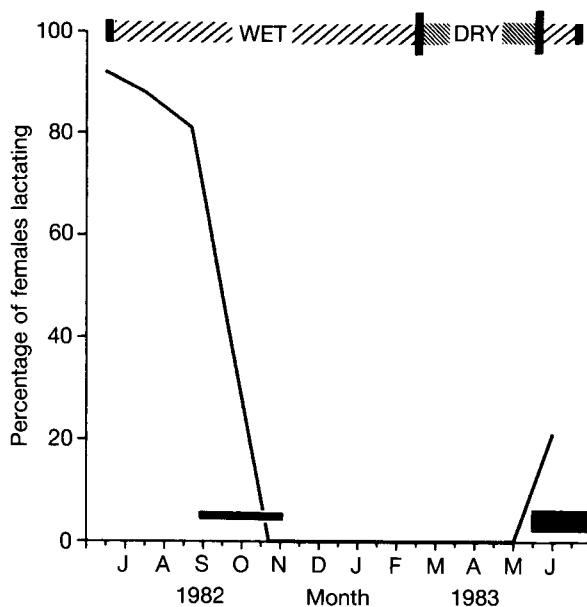
FIG. 3. Lactation in multiparous female *Haplonycteris fischeri* in 1982–83. The wide bar indicates the period of parturition; the narrow bar indicates the probable period of weaning. The wet and dry seasons (defined arbitrarily as the nine wettest and three driest months of the year) are indicated with labelled bars at the top of the figure.

FIG. 4. Reproductive condition of nulliparous and primiparous female *Haplonycteris fischeri* from Lake Balinsasayao, Negros Island, from 1979–1984. All autopsied females from late August and early September 1982 in which the ovaries and uteri had not yet enlarged are included in the 'not-pregnant' category, although only about half were examined microscopically. Most other females on the figure were examined microscopically. The wet and dry seasons (defined arbitrarily as the nine wettest and three driest months of the year) are indicated with labelled bars at the top of the figure.

within one to three weeks after parturition. The embryo underwent a post-implantation period of greatly slowed development lasting eight months, during which the embryo was detectable by palpation or autopsy as a 3–4 mm bulge in the uterus. Because development slows tremendously but does not cease completely, the developmental stage of the embryo during the delay (as determined by serial sectioning and staining of embryos) provided a rough guide to its temporal position in the delay period. In energetic terms, however, the growth during the delay period is negligible, as the conceptus increases in mass by less than 0·05 g over the course of the delay (7–8 months in parous adults). At the end of the delay, embryos developed rapidly over a three-month period to reach 25–30 mm in crown-rump length just prior to parturition (Fig. 2). With one exception, a near-term female in January, all multiparous females captured from October through February were pregnant with embryos in delay. Samples of *Haplonycteris* from the Luzon site are sufficient to demonstrate the occurrence of a similar developmental delay in that population as well (Fig. 7c).

The timing of development in the embryos of primigravid females on Negros was slightly different (Fig. 4). Most females born in June were pregnant by October or November, at 5–6 months of age. Their embryos implanted and then entered a delay phase lasting about 3–4 months, ending about two weeks later than in multiparous adults.

On Negros, copulations occurred through most of the year; females that were not pregnant, or that carried embryos that had not yet reached the delay stage, were found from May through March. Sperm were found in the testes and epididymides of adult males in all months of the year. Similarly, testis volume in adult males did not vary significantly during the year, although mean testis volume was highest in May and June, the months when almost all parous females ovulated.

A proportion of the embryos sectioned were in some way abnormal. One of 10 females with pre-implantation zygotes or blastocysts held a disintegrating morula in the oviduct ipsilateral to an
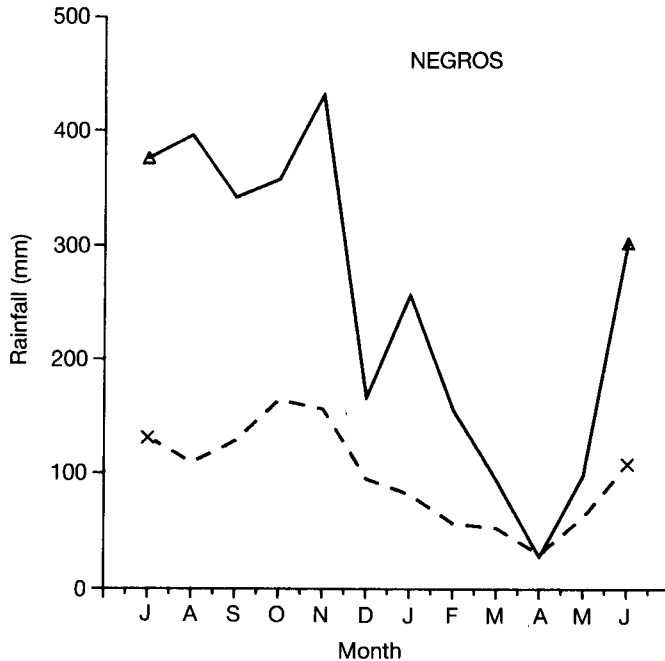
FIG. 5. Mean monthly rainfall on Negros Island at Dumaguete City for 1958–1983 (Dumaguete City Weather Station) and mean monthly rainfall at Lake Balinsasayao for July 1982–June 1984 (Heideman, pers. comm.; Cadelina, unpubl. manuscript). △ Balinsasayao; X Dumaguete City.

ovary containing a normal corpus luteum. Eleven of 105 embryos examined in implantation or in delay had abnormal features. Five of these contained abnormal cells, or had regions where layers of ectoderm or endoderm were either replaced by morphologically different tissue or had large gaps. Two contained inner cell masses lacking the distinct pattern of organization of normal embryos, but in both of these cases the abnormalities could have been artefacts of processing. The remaining four concepta contained apparently normal embryos but had a second, smaller embryo that was clearly abnormal within the yolk sac. This suggests that at least 5–10% of all embryos have abnormalities; the figure may be much higher, as some females sampled could have lost or resorbed several embryos before my sampling. It is not clear what proportion, if any, of these embryos would have failed to complete development.

The fact that a delay period can be inferred for all females on Negros strongly implies that a delay following implantation is obligate in the normal course of development. The evidence suggests that, at a particular stage of development, all embryos enter a period of delay. The duration of the delay is apparently not constant, as females were impregnated over more than half of the year on Negros, yet parturition was relatively synchronous in May and June (Fig. 2). This implies that some cue around March (on Negros) ends the delay for all females. If this is so, then the timing of the entire reproductive cycle is determined by that single event in or near March, when the period of delay ends.
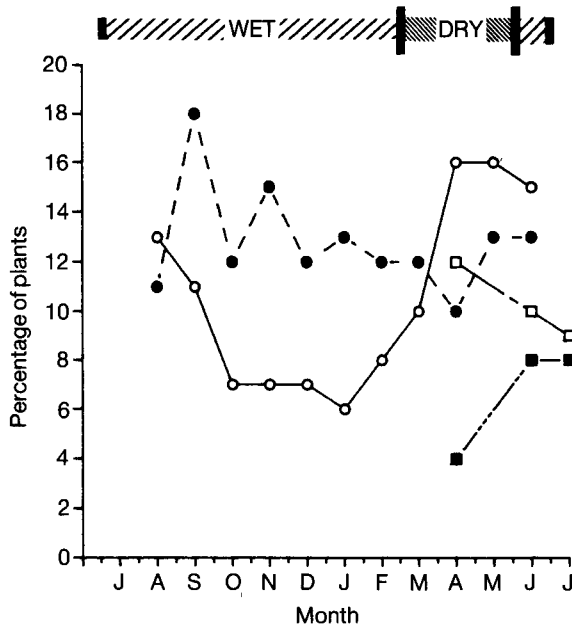
FIG. 6. Percentage of plants surveyed in flower and in fruit at Lake Balinsasayao, Negros Island, from August 1982–June 1983 and April, June and July 1984 (sample size is approximately 480 plants in most months, range 295–515). The wet and dry seasons (defined arbitrarily as the nine wettest and three driest months of the year) are indicated with labelled bars at the top of the figure. O Flowering, 1982–83; ● fruiting, 1982–83; □ flowering, 1984; ■ fruiting, 1984.

Reproductive timing and environmental correlates

The time of parturition for multiparous females on Negros (late May and June) was the same in all five years (Fig. 2). The period of parturition fell within the average transition period between dry and wet seasons on south-eastern Negros (Fig. 5). The actual timing and duration of wet and dry seasons during the years of the study varied greatly, from an extremely long dry season of five months in 1983 (a drought associated with *El Nino*), to a truncated, one-month dry season in 1984. Because of this annual variation in rainfall pattern, parturition coincided with the dry-wet transition in only three of the five years of sampling; in the other two years, parturition occurred one or two months following the transition. Parturition in late May and June would have fallen outside the transition in approximately one-third of the last 26 years, preceding or succeeding the transition by one to three months.

Seasonal variation in flower and fruit abundance was not pronounced; variation in percentage of all plants in flower or fruit between any two months was generally less than two-fold. In addition, the data suggest substantial differences in annual patterns in some years. Significantly more trees and palms flowered in the dry season than in the wet season, but this was not true for vines (Fig. 6). There was a non-significant tendency toward more fruiting in the wet season for most plant classes. The proportions of plants in flower or fruit in most plant classes were generally lower in 1984, which had a truncated dry season, than in 1983, a year with an extended dry season (Fig. 6). Patterns of average number and volume of flowers or fruits per plant or per unit area were generally, but not always, similar to patterns of percentage flowering or fruiting (Heideman, 1987).

On average, late pregnancy, lactation and weaning occurred in the late dry season and early wet season, which were periods of peak overall flower and fruit abundance in 1982–83 (Fig. 6). Fruiting was maximal during the early part of the wet season in 1982 (but not different, statistically, from the rest of the year), and flowering peaks occurred near the dry-wet transition in both 1982 and 1983 (Fig. 6). Such patterns are common at dry-wet season transitions in tropical habitats (Janzen, 1967; Foster, 1982a, 1985). However, following the unusually high rainfall in the dry season of 1984 (Cadelina, unpubl. manuscript), the percentage flowering and the percentage fruiting for some groups of plants were lower during the latter part of the dry season and the beginning of the wet season. This can be seen from the means of the percentage of palms and of three categories of trees in flower and fruit (Fig. 6). In that year, the dry period may have been too short to trigger reproduction in some plant species or individual plants (see Foster, 1982b). The lower flowering and fruiting levels in 1984 may have caused the observed high mortality rate of young bats. In that year, 33% (10 of 30) of the post-parturient females captured during the time of lactation in June and July 1984 (prior to weaning in September and October) were not lactating, compared to only 12% (5 of 40) in 1982 (G-test with William's correction for small cell sizes, $G = 4.23$, $P < 0.05$), implying much higher juvenile mortality in 1984. This suggests the importance of climate and flower/fruit abundance to successful reproduction.

In many mammals, weights of females decline during periods of lactation and weaning, and weights of males decline during periods of mating. In *Haplonycteris*, the adjusted weight of parous females with uterine swellings of 5 mm or less did not vary significantly between any months (one-way analysis of covariance, using forearm length as the covariate to adjust for size; $P > 0.1$ for test of equality of adjusted means, and for all comparisons between periods of lactation and periods of non-lactation). In contrast, the weights of adult males varied significantly over the year (one-way analysis of covariance, using forearm length as the covariate; $P < 0.001$ for test of equality of adjusted means). The greatest difference in mean adjusted weight between any two months was 2·3 g (13% of body weight). A pre-planned comparison of male weights between the period when most females became sexually receptive (May–October) and the period when very few females became sexually receptive (November–April) showed significantly lower male weights during the period when most matings occurred (one-way analysis of covariance, using forearm length as the covariate; $P < 0.05$ for equality of adjusted means for pre-planned contrast of months). The difference in average weight between these two periods was 0·90 g (5% of mean body weight).

Geographic variation in reproductive timing

At the northern Luzon site, the drier part of the year ends three months later than on Negros (Figs 7a and 5); thus, parturition is not expected to be concurrent at the two sites. However, four female *Haplonycteris* with 17–21 mm embryos captured on Luzon in May 1981 (Fig. 7c) would have undergone parturition in mid-June synchronously with females on Negros, assuming similar post-delay development rates. Average annual rainfall at the Luzon site is almost three times that of the Negros site, and probably all of the months at the Luzon site are wet enough for moisture stress on plants to be rare, and there may be no physiological dry season (see Brunig, 1971). Because rainfall levels in all months are high, it may be inappropriate to term the months of relatively lower rainfall a 'dry season', but there is still no reason to expect concurrent reproductive events between the two sites.
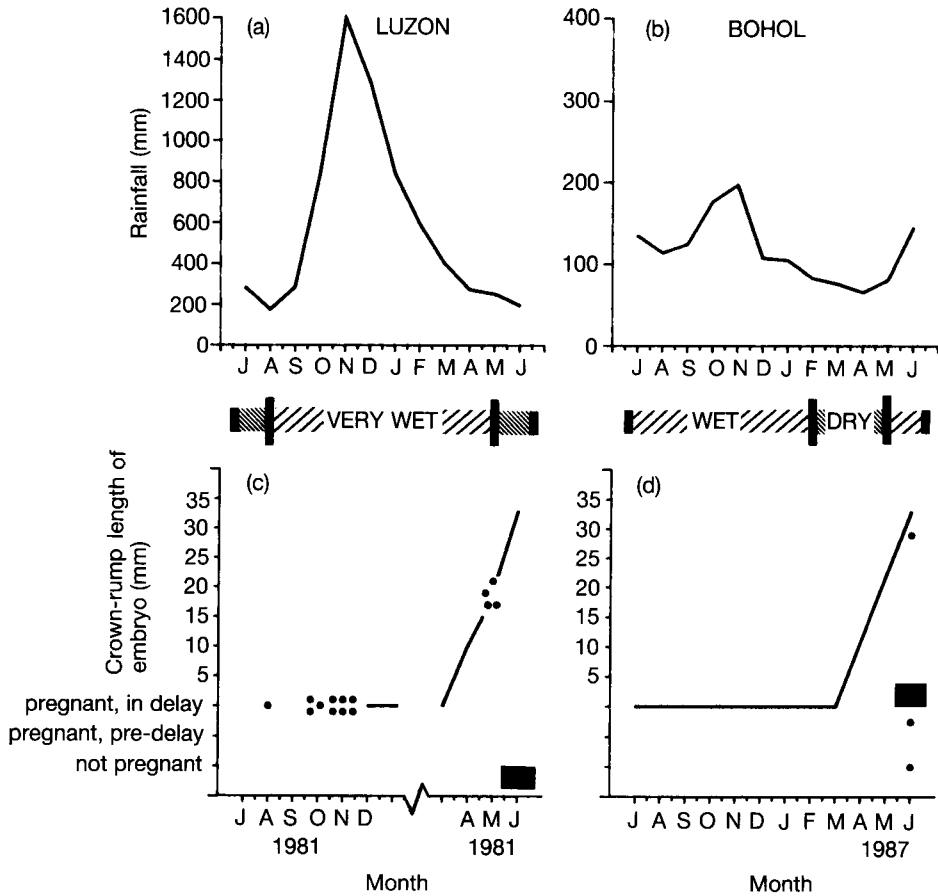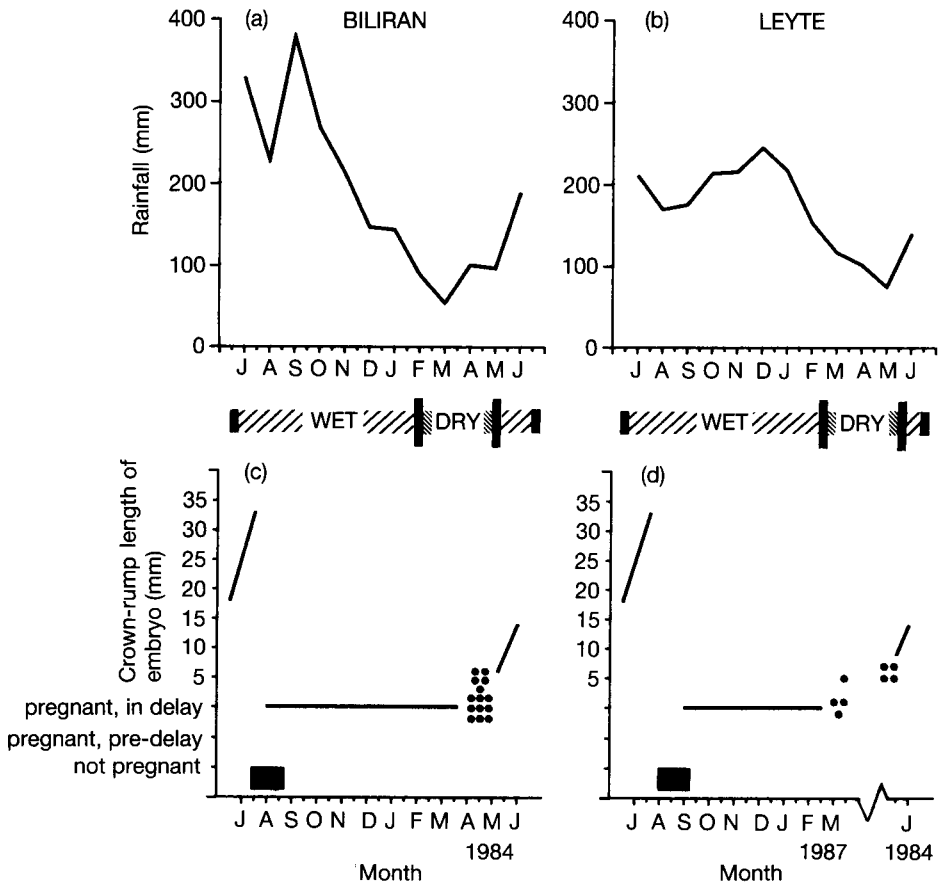
FIG. 7. Mean monthly rainfall and reproductive status of parous adult *Haplonycteris fischeri* on Northern Luzon and Bohol in the Philippines. Each dot represents a single female. The wide black bars on c and d indicate the period of parturition. The reproductive tracts of all females from Luzon were examined microscopically, those from Bohol were not. The wet and dry seasons (defined arbitrarily as the nine wettest and three driest months of the year) are indicated with labelled bars. (a) Mean monthly rainfall 20 km from the Isabella Province site at Maconacan, Isabella Province, Luzon for January 1976–March 1981 (data from Acme Plywood and Veneer Company). (b) Mean monthly rainfall 28 km from the Bohol site (Tagbilaran; 1961–1980) (data from the Philippine National Weather Bureau). (c) Reproductive condition of female *Haplonycteris fischeri* from Isabella Province, Luzon in 1981. The four females captured in March 1981 are shown on the right side of the graph to facilitate comparisons with other figures. (d) Reproductive condition of female *Haplonycteris fischeri* from Bohol Island in June 1987.

The Biliran, Leyte and Bohol sites are similar to the Negros site in amount and distribution of annual rainfall (Figs 7b, 8a, b and 5). Females in these three populations would be expected to undergo parturition concurrently with those on Negros. In fact, parturition occurs two to three months later on Biliran and Leyte than on Negros. Fourteen females captured between 28 April and 2 May in 1984 on Biliran Island had embryos that were either near the end of the delay or had resumed rapid development (Fig. 8c). A second Biliran sample of 13 parous adult females taken

FIG. 8. Mean monthly rainfall and reproductive status of parous adult *Haplonycteris fischeri* on Biliran and Leyte in the Philippines. Each dot represents a single female. The wide black bars on c and d indicate the period of parturition. The reproductive tracts of all females represented on this figure were examined microscopically. The wet and dry seasons (defined arbitrarily as the nine wettest and three driest months of the year) are indicated with labelled bars at the top of the figure. (a) Mean monthly rainfall 10 km from the collecting sites on Biliran (1978–1986) (data from the Philippine National Weather Bureau). (b) Mean monthly rainfall 10 km from the Leyte site (Baybay, 1971–1986) (data from the Philippine National Weather Bureau). (c) Reproductive condition of female *Haplonycteris fischeri* from Biliran Island in April 1984. A second sample of 13 parous adult females obtained in April 1987 contained an almost identical distribution of embryo sizes (conceptus sizes [mm] 3, 3, 3, 4, 4, 4, 4, 4, 5, 5, 6, 6 and 7). (d) Reproductive condition of female *Haplonycteris fischeri* captured near the Visayas State College of Agriculture, Baybay, Leyte in May 1984 and March 1987.

between 10 and 25 April 1987 showed a similar distribution of embryo sizes (Fig. 8c). If these embryos had developed at the same rate as those on Negros, parturition would have occurred in August, one to two months following the dry-wet transition on Biliran (Fig. 8a). Four females examined on Leyte Island in late May held embryos at about two to three weeks after the end of the delay (Fig. 8d), and would have undergone parturition in late August or early September, in the middle of the wet season (Fig. 8b). On Bohol, however, three females captured in June held near-

term embryos or had recently given birth (Fig. 7d). At this site, parturition occurred synchronously with parturition on Negros, also falling in the transition from dry to wet season (Fig 2, 5, 7b and d).

A second seasonal climatic factor potentially affecting the timing of reproduction is the annual cyclone season, June through November. Seventy-five percent of all cyclones occur during those months, with a peak of 20% of the total in August (Thorp, 1962; and see Heideman, 1987). Typhoons bring up to several days of high, gusting winds and rain during which *Haplonycteris* activity is strongly reduced (unpubl. data). Since captive animals that do not eat become very weak and may die after 24 hours, several days of greatly restricted foraging and low temperatures are likely to be a significant risk to both mother and offspring. Strong winds and rain from cyclones affect the Luzon, Biliran, Leyte and Bohol sites about three to six times per year, on average, and the Negros site one to two times per year (Thorp, 1962). Despite the potential impact of cyclones on reproductive success, *Haplonycteris* at all sites undergo late pregnancy, lactation and, at two sites, weaning within the cyclone season.

The periods of late pregnancy, lactation and weaning overlapped with the period when migratory avian competitors and predators were most abundant (October–March) on Biliran and Leyte, but did not overlap at all on Negros, Bohol or Luzon.

Discussion

Advantages of a delay period

Several kinds of reproductive delay extending the period between copulation and parturition are found in a wide variety of mammals (Diprotodonta, Insectivora, Chiroptera, Edentata, Carnivora, Artiodactyla and Rodentia; Renfree & Calaby, 1981). Delayed implantation is found widely in the Mammalia, sperm storage is the norm in temperate-zone bats (Racey, 1979), and delayed (or 'retarded') development has been demonstrated in three species of bats (Phyllostomidae–Bradshaw, 1961, 1962; Fleming, 1971; Burns, Baker & Bleier, 1972; Rhinolophidae–Bernard & Meester, 1982), and implicated in several other species of bats (Pteropodidae–Krishna & Dominic, 1983; Rhinolophidae–Ramakrishna, 1977; Emballonuridae–Krishna and Dominic, 1982; Natalidae–Wimsatt, 1975; Vespertilionidae–Medway, 1971). Given that delays have apparently arisen independently numerous times within the Mammalia, and that delays may reduce fitness by reducing the absolute number of offspring produced by a female, it is reasonable to search for adaptive explanations for delay periods. At least six hypotheses can be advanced for the adaptive significance of delays, along with an alternative hypothesis of no current adaptive significance (Gould & Lewontin, 1979; Dobson, 1986). Hypotheses on the adaptive significance of delays are not necessarily restricted to any single type of delay, and I will consider all of them in relation to *Haplonycteris*.

First, a delay period may allow females to respond more rapidly to some environmental cue that predicts good conditions in the future. In desert-dwelling macropodids, a delay allows females to respond more rapidly to the favourable conditions following rain (e.g. Newsome, 1965). In *Haplonycteris*, the prior completion of mating and three weeks of development would allow females to respond one month sooner to a predictor of good conditions. This attractive hypothesis can be rejected in the case of *Haplonycteris*, however, given that during five years of study the

timing of parturition varied by less than a few weeks between years despite widely differing rainfall, the only climatic variable with significant seasonal variation (Fig. 2).

Secondly, in some species, a delay allows mating at a time when males are either most readily available, or in periods when the relative qualities of males as mates can best be judged. For example, pinnipeds generally undergo a post-partum oestrus, with delays in implantation of up to four months (Daniel, 1981). Mating takes place at the only time of the year when females are obligated to aggregate, and males can perhaps be evaluated or exploited as defenders against conspecifics or predators. In *Haplonycteris*, however, males are present and producing sperm throughout the year. There is no reason to believe that there is some best time to mate, given that all first-year females and at least one multiparous adult became pregnant between July and January. Thus, there is no evidence to support the hypothesis that the function of the delay is to synchronize male and female mating periods in *Haplonycteris*.

Thirdly, in many rodents, a facultative delay in implantation induced by lactation allows females to avoid suckling two litters at the same time (Clutter, 1978). Because the delay in *Haplonycteris* occurs in non-lactating multiparous females as well as in primigravid young females (Heideman, 1987), this is an unlikely explanation for the delay.

Fourthly, a delay may simply be an alternative to using a period of reproductive quiescence to time lactation and weaning appropriately (Clutter, 1978; Racey, 1982). In this case, the delay is functionally equivalent to such a period of reproductive quiescence, with the difference that the timing of parturition is controlled by the cue ending the delay rather than by the timing of mating. Along these lines, Fleming (1971) argued that the delay in *Artibeus jamaicensis*, occurring in one of two pregnancies during the year, allows females to lactate and wean their young during the two periods of food abundance. The period of lactation and weaning in *Haplonycteris fischeri* coincided with a period of high overall flower and fruit availability in 1982, but apparently not in 1984 (Fig. 6). There was evidence that reproductive success was lower in the poor year, 1984, when significantly more females halted lactation prematurely, probably indicating the death of their young. On average, parturition and lactation occur at the end of the dry season and the beginning of the wet season, periods when flowers and fruits are most abundant in many tropical forests (Janzen, 1967; Foster, 1985). A delay period is not necessary to achieve this pattern of timing. A post-partum period of reproductive quiescence followed by the initiation of mating in February would produce the same result, and similar patterns of seasonal monoestry are accomplished without a delay by most seasonally monoestrous pteropodids. This hypothesis, that the delay is a mechanism to time lactation and weaning appropriately, is reasonable for *Haplonycteris*.

As a fifth alternative, Racey (1982) suggested that sperm storage may function to synchronize parturition and lactation in species where copulations are relatively asynchronous; delayed implantation or development could serve the same purpose. Such synchrony can be advantageous if: (1) the bats derive energetic benefits from clustering; (2) predators are so satiated by the sudden abundance of clumsy, weak young bats that a greater proportion of the young survive the few months of their lives when they are most vulnerable to predators (Janzen, 1976); or (3) there is some kind of optimum period for reproduction, with resulting greater survival of mother and young. For *Haplonycteris*, greater synchrony is certainly a result of the delay, but there is no evidence regarding either costs or benefits of synchrony for the species.

A sixth hypothesis apparently unexamined previously is that a post-implantation delay may allow females to evaluate the quality of their embryos. In this case a female could resorb a defective embryo and restart pregnancy without losing a reproductive opportunity. In the absence of a delay, the loss of an embryo within the first three weeks of pregnancy would cause the female to

undergo parturition at least one month later than otherwise, perhaps at a suboptimal time. The presence of morphological abnormalities in the embryos of about 10% of the females examined implies a significant number of non-viable embryos. The parous female captured in March with an unimplanted blastocyst and very early corpus luteum had a corpus albicans in the contralateral horn, indicating recent termination of pregnancy. It may be significant that the range of *Haplonycteris* includes a great many small islands. A delay period might be a significant advantage to a species in which colonization by small groups is followed by a period of high inbreeding, with a probable increase in the frequencies of homozygous recessive lethal genes. The increase in fitness from the ability to resorb defective embryos may be very important to an animal whose lifetime includes only a few opportunities to produce offspring.

The hypothesized benefits of a delay are not mutually exclusive; several could simultaneously provide an advantage. For *Haplonycteris fischeri*, three of the hypotheses above are consistent with the data: (1) the delay functions to synchronize parturition among females; (2) the delay is simply an alternative to reproductive quiescence as a mechanism to achieve a particular pattern of reproductive timing; and (3) the delay allows defective embryos to be resorbed and a second embryo to be produced, increasing the probability of reproductive success. The cost of a delay to the female seems to be slight. The extra mass of embryo, extraembryonic membranes, and uterine tissue amounts to less than 0·25% of her body mass, and during the delay they are probably among the slowest growing and least active tissues in her body.

Age-specific variation in reproductive timing

Why should reproductive timing be different in primigravid females? The delay apparently ends slightly later in primiparous females than in adults, and the last part of pregnancy appears to require up to two weeks longer in these yearling females. As a result, parturition in yearling females may occur as much as one month later than in adult females. Young females may be on a lower quality diet because of their inexperience, and poor nutritional status can result in decreased developmental rates. Thus, parturition might be delayed in primigravid females because of a slower response to the cue ending delay and to slower post-delay developmental rates. A second possibility is that nulliparous females are maximizing their own survival by timing reproduction such that late pregnancy and lactation occur at the most favourable time for their own survival, at a cost of reducing the probability of survival of their young by weaning them when food abundance has already begun to decrease (Bradbury & Vehrencamp, 1977). However, in this case some parous females in poor condition should also undergo later parturition, and there was no evidence for this.

Significance of patterns of reproductive timing

It is important to note that at the two sites where the time of parturition could be determined for more than one year, parturition occurred at the same time in each year. This was true in two years on Biliran, 1984 and 1987 (Fig. 8c), and in five years on Negros; 1979, 1981, 1982, 1983 and 1984 (Fig. 2). This suggests that it is reasonable to use data from a single year to establish the timing of reproductive events at localities where only a single season's data were obtained.

Rainfall

Reproduction is seasonally restricted on Negros, as late pregnancy, lactation and weaning occur only from April through October. On average, lactation and weaning occur during the early part of the wet season, which was the period with the greatest overall resource abundance in 1982 and 1983. The period of lactation fell within a period of somewhat reduced flowering and fruiting in the unusually wet year of 1984, and there was evidence that fewer females successfully weaned young in that year (see **Results**).

On Negros, reproductive timing of *Haplonycteris* had the effect of synchronizing lactation and weaning with the time of the year when, on average, the early wet season occurred. The timing of the early wet season varied between years, and was not very predictable within a year. Although bats might benefit from better synchronization of reproduction with a particular point in the rainfall cycle, it appears that accurate prediction of the timing of seasons is not possible within a given year. The timing of the wet and dry seasons on southern Negros is only moderately predictable using either current rainfall or mean monthly rainfall as predictors of future rainfall (Heideman, 1987). The existence of a drier season is a fairly predictable event in each year; at Lake Balinsasayao, there should be, on average, a two-month dry season, usually centred around April. Mean monthly rainfall for a given month in previous years is either equivalent to or better than rainfall in the preceding months as a predictor of rainfall in the current year (Heideman, 1987). Thus, if rainfall is locally important, the best the bats can achieve may be reproduction at the time that, on average, is the most favourable. The lack of between-year variation in reproductive timing in *Haplonycteris* on Negros is consistent with this result.

Populations of *Haplonycteris* on different islands did not time reproduction to coincide with the same stage of the annual rainfall cycle, and this hypothesis can be rejected. Despite very different rainfall patterns, reproduction by the populations on Negros and Luzon is apparently synchronous. Rainfall patterns at the other three sites are similar to that of Negros, and on Bohol, reproduction is synchronous with that on Negros. However, on Leyte and Biliran, reproduction is delayed by two to three months relative to Negros populations. These observations indicate that the timing of rainfall does not in itself directly control reproductive timing.

Cyclones

Late pregnancy, lactation and, at two sites, weaning fell within the cyclone season. Thus, reproduction is not timed to avoid the cyclone season.

Avian migrants

The periods of late pregnancy, lactation and weaning overlapped with the period when migratory avian competitors and predators were most abundant (October–March) on Biliran and Leyte, but did not overlap at all on Negros, Bohol or Luzon. Thus, the hypothesis of avoidance of avian competitors and predators is inconsistent with the timing of reproduction in *Haplonycteris fischeri* at two of the five sites, and the hypothesis can be rejected.

An alternative: local plant phenologies

The phenologies of plants at most tropical sites are generally related to rainfall patterns and controlled to some extent by rainfall and other climatic events (Augspurger, 1982; Borchert, 1983). However, because plant species' composition and abundance are likely to vary between islands,

the plant species upon which *Haplonycteris* depends for food also are likely to vary between islands. Additionally, *Haplonycteris* may be similar to neotropical frugivorous bats in relying heavily on a very few species of fruits during lactation (Dinerstein, 1983). Especially in geographical areas where strong seasonal climatic change is lacking, the timing of flowering and fruiting peaks in locally important plant species could result in temporal divergence in resource abundance not directly related to climate. Differing resource phenologies would, in turn, result in selection for different patterns of reproductive timing for *Haplonycteris fischeri*, even under similar annual patterns of climate. Thus, reproductive timing may be determined by adaptation to the local phenological patterns of the resources upon which the bats rely.

If *Haplonycteris* are reproducing optimally, then the factors determining optimum reproductive periods are not clearly related to rainfall patterns. Nevertheless, *Haplonycteris* reproduce seasonally; this suggests that seasonality is important in these habitats where climate is only moderately seasonal, but implies that reproductive seasonality may be an evolutionary response induced by site-specific factors rather than by ubiquitous community-wide responses to seasonal climatic fluctuation. Thus, the practice of using local rainfall patterns combined with ecological correlates of rainfall established elsewhere to infer the reasons for local reproductive timing may produce misleading results.

Summary

Haplonycteris fischeri in the Philippines have a single young at the same time each year. Most multiparous females become pregnant shortly after parturition in May or June, but some multiparous females, and all females born in the previous May or June, become pregnant over the following six or seven months. Embryos enter a delay period after implantation; in the great majority of cases, the delay ends in March or April, regardless of the time of copulation, thus synchronizing the time of parturition among females. The delay may be important in setting the timing of parturition at a particular time of year or in synchronizing births (perhaps to adjust reproductive timing to the energy and protein intake available from the frugivorous diet), but it may also allow females to resorb defective embryos without losing the chance to reproduce. Late pregnancy, lactation and weaning occurred during the end of the dry season and early wet season, and coincided with peaks in flowering and fruiting. However, populations on different islands did not time reproduction to coincide with the same point in the annual rainfall cycle, indicating that rainfall is related to reproductive timing only indirectly, if at all. However, it is quite possible that reproductive timing is related directly to the fruiting and flowering phenologies of particular plant species, and that the specific phenological patterns of the plant species that are locally important to *Haplonycteris* are directly related to rainfall patterns. Pregnancy, lactation and weaning were not timed to avoid the cyclone season or the period when migrant avian predators or competitors were most abundant, and these factors can be rejected as possible causes of reproductive timing for *Haplonycteris* on these islands. The patterns of reproduction seen suggest that seasonality may be induced by site-specific factors rather than by ubiquitous community-wide responses to seasonal climatic variation. The extreme seasonality of reproduction of these populations in five relatively aseasonal sites implies that seasonality remains important even where seasonal changes are mild.

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