Environmental Determinants of Birth Seasonality in Night Monkeys (*Aotus azarai*) of the Argentinean Chaco

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*The night monkeys (*Aotus azarai*) of Formosa, Argentina provide an opportunity to investigate the influences of ambient temperature and photoperiod on reproduction in a highly seasonal environment: the Chaco. Between 1997 and 2000, we collected data to evaluate the relationship between rainfall, ambient temperature, photoperiod and food availability and the annual distribution of mating behavior and births in 15 groups of monkeys in the forests of the Eastern Argentinean Chaco. Our data show that the area is highly seasonal, characterized by significant fluctuations in rainfall, temperature, photoperiod and food availability. There are two rain peaks in April and November and a dry season lasting from June to August. Monthly mean temperatures were on average 11°C lower during winter months than they were during summer months. Temperatures <10°C and >33°C were also frequent through the year. Days are 3 h longer during the summer than during the winter months. Insect abundance and the percentage of tree species producing fruits, flowers or new leaves reached a low in the coldest winter months. Mating was infrequent, and we only observed it between May and September. Half the births (n = 13) occurred during a 2-week period in October. Infant survival during the first 6 mo of life was high (96%). Our findings suggest an environmental control of reproduction. Changes in photoperiod and temperature may promote reproductive activity in females that might conceive and begin*

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pregnancy at a time void of high temperatures that could be metabolically challenging.

INTRODUCTION

The degree to which mammals constrain their reproductive efforts to certain times of the year correlates with several proximate and ultimate factors. Ambient temperature, photoperiod, rainfall, and food availability are some of several environmental factors that influence reproductive activity in mammals (Bronson, 1989). Among primates, the effects of rainfall and food availability have been widely investigated, and food availability may be the most important ultimate factor driving birth seasonality (Di Bitetti and Janson, 2000). Conversely, the influence of temperature and photoperiod on primate reproduction has received relatively little attention (Lindburg, 1987), probably because most primate species are confined to the tropics, where changes in these factors are minimal. In some of the primate genera with distributions extending out of the tropics, seasonal changes in ambient temperature and photoperiod influence their reproduction (Kawai *et al.*, 1967; Perret, 1992; Petter-Rouseaux, 1980; Sauther, 1991; Van Horn, 1975).

The night monkeys of South America (*Aotus spp*.) provide a good opportunity to investigate the influences of ambient temperature and photoperiod on reproduction of free-ranging subjects. Widely distributed from Panamá to the Argentinean Chaco, the different night monkey species are differentially exposed to a range of environmental conditions (Ford, 1994). For example, in the tropical forests of Manú National Park, Perú, *Aotus nigriceps* experience temperatures that range between the lower and upper 20s °C (Terborgh, 1983) and almost no variation in photoperiod. Conversely, in the Chaco, *Aotus azarai* experiences temperatures that are highly seasonal, frequent extreme temperatures, and a photoperiod regime that varies significantly across the year.

The effects of extreme ambient temperatures can be acute for a relatively small animal (*ca*. 1 kg) like the night monkey. A few degrees of temperature above thermoneutrality—the range of ambient temperature within which the caloric costs of homeostasis are minimized—apparently have a more profound effect on reproduction than a much greater decrease below thermoneutrality. The inhibitory effects of low temperature can normally be reversed by increasing food intake; whereas even a small increase in ambient temperature over thermoneutrality requires a whole new set of metabolic and behavioral adjustments (Bronson, 1989). Via studies on thermoregulation in night monkeys from Bolivia and Perú, and from

Brazil Le Maho *et al.* (1981) and Morrison and Simoes (1962), respectively found that the monkeys had a very narrow thermoneutral zone. They responded with dramatic physiological changes to ambient temperatures slightly $>30°C$, and with shivering at temperatures $<28°C$. If temperatures below and above the thermoneutral zone impose an energetic cost on night monkeys during certain times of the year, individuals may time reproductive events to minimize the thermoregulatory challenge. Ambient temperature is usually a poor predictor of future environmental conditions given its daily and interannual variations. Thus, an alternative mechanism may be to cue on changes in photoperiod as a way to predict favorable temperature conditions for reproduction in the near future.

We examined the annual distribution of mating behavior and births in a population of night monkeys in the seasonal gallery forests of Formosa Province in the Eastern Argentinean Chaco. Using data collected from 15 groups during 4 birth seasons (1997–2000), we evaluated the relationship between various environmental cues—rainfall, ambient temperature, photoperiod and food availability—and the timing of mating behavior and births. Given that night monkeys in the Chaco seem to adjust their periods of activity to changes in temperature and photoperiod (Arditi, 1992; Fernandez-Duque and Bravo, 1997; Rotundo *et al.*, 2000; Wright, 1985), we predicted that their reproductive activity is also influenced by the particularly seasonal conditions of the area.

METHODS

Study Area and Population

The area, which comprises a mosaic of grasslands, savannas, dry and gallery forests, is located outside of the tropics at the southern end of the distribution range of *Aotus* (58° 11′ W, 25° 58′S). The semideciduous gallery forest along the banks of the Riacho Pilagá in the Eastern Chaco of Argentina (Placci, 1995), is home to *Aotus azarai azarai*, which inhabits the provinces of Formosa and Chaco, Argentina (Brown and Zunino, 1994).

Night monkeys are socially monogamous and normally live in relatively small groups (Wright, 1985, 1994). The study population includes 11 neighboring social groups, which range between three and seven individuals. Group and individual densities in the area are 16 groups/km^2 and 64 ind/km^2, respectively. In March 2000, one third of the population consisted of infants and juveniles, while the remaining two-thirds were adult-size individuals. Fernandez-Duque *et al.* (2001) provided a detailed description of the demography and structure of the study population.

The diurnal activity of the population (Rotundo *et al.*, 2000) provides a unique opportunity to obtain accurate information on the timing of births and mating activity in an otherwise nocturnal genus.

Data Collection and Analysis

Rainfall, Temperature and Photoperiod

We obtained mean monthly rainfall data (1977–2000) from records at Estancia Guaycolec. We recorded temperature hourly via a Stowaway XTI temperature data logger between August 11, 1998 and August 16, 1999.

To estimate monthly changes in photoperiod, we relied on light intensity data collected with a Stowaway Light Intensity Logger exposed horizontally to direct sunlight. The data logger recorded light intensity every 15 min during one year (August 11, 1998 to August 10, 1999). We calculated changes in monthly photoperiod via the light intensity records of the 15th day of each month. We calculated the number of daylight hours—photoperiod—as:

$$\text{Photoperiod} = \#\ \text{records with light}/4,$$

in which # records with light is the number of times the data logger recorded an intensity above its baseline (0.0015 lumen/ft^2). When we compared our light intensity records to those obtained from the U.S. Naval Observatory Astronomical Applications Department web page (http://aa.usno.navy.mil/AA/), it was apparent that the Light Intensity Logger records nautical twilight, which is the time period defined to begin in the morning and end in the evening when the sun is geometrically 12° below the horizon.

Insect Abundance

We obtained data on the availability of insects via light-traps (Smythe, 1997). A light trap comprises a light source, a collecting cone, and a bag filled with poison. A fraction of the insects attracted to the trap falls into the cone, and the poison quickly kills them. Although light-traps do not provide an absolute measure of the number of insects available in the area, the traps provide a crude assessment of seasonal changes in the abundance of those insects attracted to the traps.

We placed two light traps at 5 and 10 m on the same tree (*Myrcyanthes punges*, Mirtacea). We left each trap on all night (1800–0600 hs), on average twice per month. We collected 58 samples on 40 nights between August 20, 1998 and August 17, 1999. On 18 of the nights, we collected the samples simultaneously using both traps. We used the 36 samples to evaluate the

effect of height on insect abundance. Mean dry weight does not differ significantly for the 2 heights (5 m vs. 10 m: 6.1 vs. 6.1 gr, t = 0.092, df = 17, p = 0.927); therefore, we averaged the 36 samples for analysis.

We collected samples during different phases of the moon ($\pm$3 days) as follows: full moon (n = 9 samples), last quarter (n = 9), new moon (n = 15), and first quarter (n = 7). Since the differences in insect abundance between different lunar phases are not statistically significant [(Kruskal-Wallis analysis of variance, X^2 = 1.8, df = 3, p = 0.6, mean ranks: 17.4 (full moon), 18.4 (last quarter), 20.1 (first quarter), 23.5 (New)], we analyzed all 40 samples together to evaluate the effects of temperature and time of the year.

The effects of the moon and temperature can heavily influence the number of insects captured on a particular night (Wolda, 1978). Although we controlled for the effects of moon-phase by sampling quite evenly through the different phases, our results should be considered preliminary in discussions of their potential to illustrate seasonal variability in insect abundance.

Phenological Data

To evaluate relative changes in the density, distribution, and abundance of plant resources, we collected monthly information on forest composition and phenology from 30 plots (50 $\times$ 10 m) randomly placed in *ca*. 30 ha of forest. We sampled a total of 1.5 ha, representing 5% of the total surface used by the 5 focal monkey groups (Sloan and Fernandez-Duque, 1999).

Within each plot, we identified, tagged, and measured the circumference of all trees and lianas $\geq$10 cm DBH (Diameter at Breast Height). We randomly placed 30 smaller plots (10 $\times$ 5 m) within the larger plots to identify all plants with DBH >5 cm, but <10 cm. Each month, we noted the presence and abundance of leaves, flowers, and fruits in the crown as a percentage of the maximum possible. Five different observers collected phenological data in the following way: one set of 10 plots was always monitored by the same observer between September 1998–August 1999, and the second and third sets were monitored by two different observers each. One new observer in November 1998 and a second new observer in January 1999, replaced the two observers who had started monitoring the plots in September 1998.

Our data are from 755 trees of a total 911 that were tagged and measured. We excluded 156 trees from the analysis because they died during the study, they were not identified taxonomically, or they were extremely difficult to assess because of poor visibility. We identified 30 species of trees in the sample. A more thorough examination of the forest identified a total of 39 species/ha (Brown *et al.*, 1993; Placci, 1995), suggesting that our own sampling of the forest may adequately approximate its specific composition.

In order to illustrate general patterns of seasonal change, we only present data on the percentage of species showing each phenophase at any particular month: presence or absence of phenophase. This is a crude estimate of plant food availability without any consideration of the night monkey diet and preferences.

Annual Distribution of Mating Behavior

We collected data on mating behavior opportunistically between 1997 and 2000. Mating occurs when two adult-size individuals are in dorsoventral contact for a few seconds or more, with or without apparent thrusting. All observations of mating occurred during daytime.

Infant Birth and Survival

We report data on the timing of births in 15 groups during 3 years. We have no date of birth in 1997 or for 4 births in 1998 because the groups were not monitored intensively enough to obtain accurate estimates. The number of groups regularly monitored has increased over the years; therefore, not all groups contributed data every year.

We provide for each birth a period of birth (POB) during which we estimate it to have occurred, and an estimated date of birth (DOB, n = 27 births), which is the midpoint of the POB. We first estimated POB via data on the presence or absence of infants noted while observing the groups (n = 18 births). Sometimes (n = 9 births) this method provided inaccurate estimates if the group had not been contacted weekly or biweekly. In those cases, we narrowed down the interval via information on the developmental stage of the infant noted during a study on infant survival and development (Rotundo and Fernandez-Duque, in preparation) and data on developmental stages in night monkeys from Dixson and Fleming (1981). For 85% of births (n = 23) the POB was <2 weeks (median: 9 days, range: 2–14 days). We estimated the remaining 4 births to the nearest 17, 18, 19, and 22 days.

All of our data are presented under the assumption that there have been no abortions, stillbirths or infants born that died before we noticed them. Since there is no published estimate of stillbirths, abortions or infant death during the first few days of life for free-ranging night monkeys, we made no correction to our estimates. Although there are data on captive populations that are useful for comparative purposes (Dixson, 1994; Gozalo and Montoya, 1990; Malaga *et al.*, 1997), we chose not to use them to enhance our estimates.

Interbirth interval (IBI) refers to the interval between births in a group, not necessarily between births of the same female. The impossibility of

identifying adult females precluded assigning the IBI to a particular female. We calculated the IBI as the interval between 2 successive DOB; therefore we only considered closed-intervals. We did not include left and right censored intervals in the analysis.

We report data on infant survival for the cohorts born between 1997 and 1999. It is too early to estimate the survival of the 2000 cohort.

RESULTS

Seasonal Changes in Environmental Factors

The Argentinian Chaco is highly seasonal, characterized by significant fluctuations in rainfall, temperature, and photoperiod. Monthly average rainfall varies significantly during the year, with two rain peaks in April and November, and a relatively dry season lasting from June to August (Table I). Interannual variation in rainfall is also important in the region. Between 1977 and 1999, relatively dry years (range: 1090–1350 mm, n = 8 years) alternated with relatively wet years (1800–2100 mm, n = 8). For example, in 1997 and 2000, it rained only 44% (105 mm) and 67% (157 mm), respectively, of the historical average during the rainy month of April, whereas it rained 170% (402) and 157% (371 mm) in 1998 and 1999, respectively.

Seasonal changes in temperature were pronounced (Table I). Monthly mean temperatures were on average 11° lower during winter months (May–August 1998) than during summer months (December–March). Extreme low and high temperatures were also frequent. Daily minimum temperatures <10°C occurred between April and September; whereas maximum daily temperatures >33°C were concentrated between September and March.

Photoperiod changed across the year. Days were >3 h longer during the summer (December–January) than during the winter months (June–July, Table I).
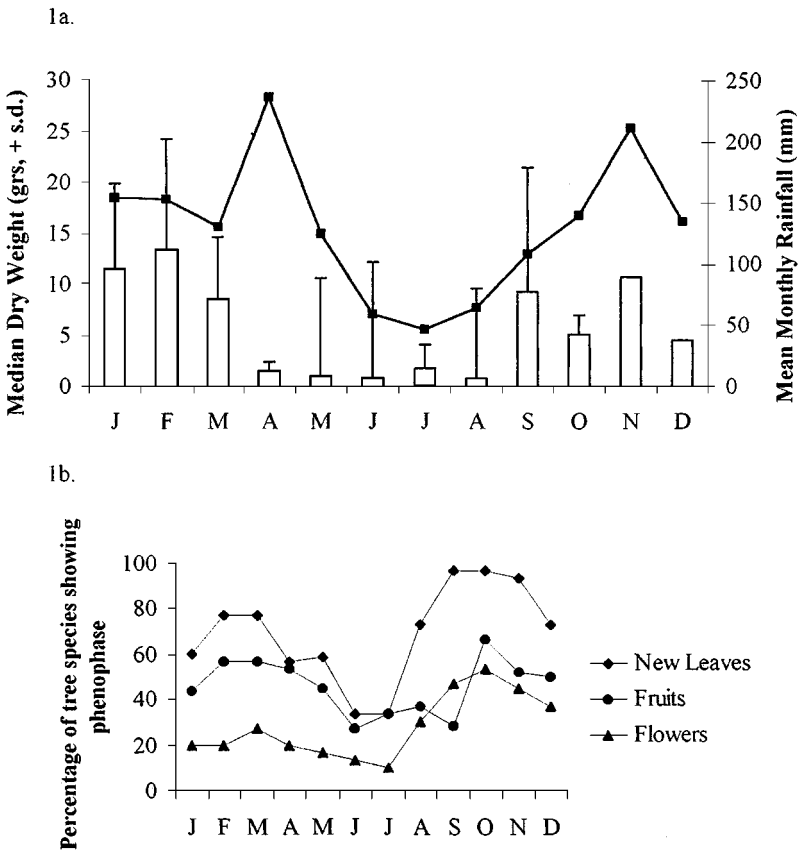
Table I. Seasonal changes in ambient temperature and photoperiod in Guaycolec, Formosa, Argentina[a]

	J	F	M	A	M	J	J	A	S	O	N	D
Monthly mean temp.	27	27	27	21	17	16	15	16	19	23	25	26
Mean max temp. (°C)	34	34	34	26	23	21	20	24	26	31	32	33
Mean min temp. (°C)	21	22	22	18	12	12	11	10	13	17	19	20
# days with Tmin < 10°C	0	0	0	4	9	11	16	5	5	0	0	0
# days with Tmax > 33°C	22	20	18	0	0	0	0	0	4	11	17	18
Day length (hrs.)	15.4	14.7	13.9	13.2	12.6	12.3	12.4	12.9	13.6	14.4	15.2	15.7

[a]Data were recorded between August 1998 and August 1999.

Seasonal Changes in Food Availability

The relative abundance of insects changed through the year (Fig. 1(a)). The weight of captured insects is considerably higher between September and March than between April and August (Kruskal-Wallis, $X^2 = 20.2$, df $= 11$, p $= 0.04$). Despite the unquestionable seasonal changes in median abundance, the abundance of insects may change drastically within days as a result of the dramatic temperature fluctuations characteristic of the area. For example, we collected 18 g of insects on September 11, but only 0.6 g 10 days later. The difference between the 2 samples is more readily explained

1a.

1b.

Fig. 1. (a) Seasonal changes in dry weight of insects and mean monthly rainfall (1977–1999). (b) Seasonal changes in the percentage of tree species with new leaves, fruits and flowers and timing of mating and birth season.

by the different temperatures prevailing on each night than by differences in the amount of moonlight. Contrary to expectations, we collected fewer insects when there was a new moon (September 21), than when the moon was nearly half-illuminated (September 11). Conversely, September 11 was a relatively warm day with temperatures of 29°C and 22°C at dusk and dawn, respectively, whereas September 21 was much cooler with temperatures of 19°C at dusk and 7°C on the following dawn. In conclusion, the data show that temperature can sometimes override moonlight effects.

We also detected a considerable degree of seasonality in the availability of new leaves, fruits and flowers (Fig. 1(b)). The percentage of tree species producing fruits, flowers or new leaves reaches a low in the coldest and driest months of June and July, whereas a higher percentage of species produce fruits, flowers and new leaves beginning in September. These findings are generally agree with findings of a previous study in the same forest (Placci, 1995).

Despite the general pattern of a decreasing number of tree species fruiting in the fall (May–June), there are ≥3 species bearing fruit then: the palm *Arecastrum rhomanzofolium* (n = 6 sampled trees), one *Ficus spp.* (n = 4), and the aguaí *Chrysophyllum onocarpum* (Sapotacea, n = 34). The small sample sizes for the first 2 species preclude analysis of the data. An analysis of seasonal changes in *Chrysophyllum onocarpum* revealed that the trees had small green fruits in April and mature fruits beginning in the second half of May. The maturation rate of fleshy fruits, like the ones produced by *Chrysophyllum onocarpum*, is dependent on the amount of rain that falls during April (Placci, 1995). In Placci's study, maturation of fleshy fruits was more abundant following the rainy April, 1990 (513 mm) than after the relatively dry April, 1989 (183 mm).

The fruits eaten from the 3 species represented 50% of all records for fruit eating during fall and winter in a previous study (Arditi, 1992). Our preliminary examinations of dietary preferences by night monkeys (in preparation) suggest the same dietary preference. They ate significant amounts of mature fruit of *Chrysophyllum onocarpum* during late May and early June of 1999; when females were conceiving.

Seasonal Distribution of Mating Behavior

We observed mating behavior infrequently, though mating behavior might have occurred during the night. Over a 3-yr period and >2,000 h of observations, we only observed mating 8 occasions (n = 5 groups). We noticed mating once in May and September, and twice in June, July and August. Assuming a gestation interval of 133 days (Hunter *et al.*, 1979), births would then be expected between October and January. The only mating observed

by Wright (1994) during her study of night monkeys in the Paraguayan Chaco occurred in August. Further evidence for the infrequent mating behavior of night monkeys comes from studies in captivity (Dixson, 1994).

Mating occurred during pregnancy ≥3 times: an infant was born in group CC only 6–7 weeks after mating on August 23, 1998; an infant was born in group D100 only 10–11 weeks after mating on July 22, 1999; and, an infant was born in Group F1200 only 7–8 weeks after mating on September 17, 2000. These observations conform with observations of mating behavior during pregnancy in captivity (Hunter *et al.*, 1979).

Seasonal Distribution of Births and Infant Survival

We report the births of 39 infants in 15 groups between 1997 and 2000 (Table II). Groups never had more than one infant born per year, suggesting the presence of only one reproductive female in each group. On average, three-fourths (76%) of the groups produced infants annually. Five of the focal groups observed since 1997 (n = 10 groups) had infants every year; whereas the remaining groups had infants in 3 (n = 2), 2 (n = 1) or 1 yr (n = 2).

We report periods of birth (POB) and dates of birth (DOB) for 27 of 39 births. Most births (88%, n = 24 births) occurred during an 8-week period between late September and late November (Fig. 2). Half of all births

Table II. Births recorded during four birth seasons (1997–2000)

Group ID	1997[a]	1998	1999	2000
A900	NA	NA	1	1
B68	NO	1	NO	1
Camp	1	1[a]	1	1
CC	1	1	1	1
CO	1	NO	1	1
Corredor	NA	NA	1	1
D100	NO	NO	1	NO
D1200	1	1	1	1
D500	1	1	1	NO
D800	NA	1	1	NO
E500	1	1	1	1
F1200	1	1[a]	1	1
Intruso	1	NO	NO	NO
Picada Casco	NA	1[a]	1	NA
Sur de G	NA	1[a]	NO	NA
# of births	8	10	12	9

Note. NA: the group was not regularly monitored to determine if a birth occurred or not. NO: group regularly monitored, but no birth recorded.
[a] All births in 1997 and 4 in 1998 could only be estimated to occur between October and December.
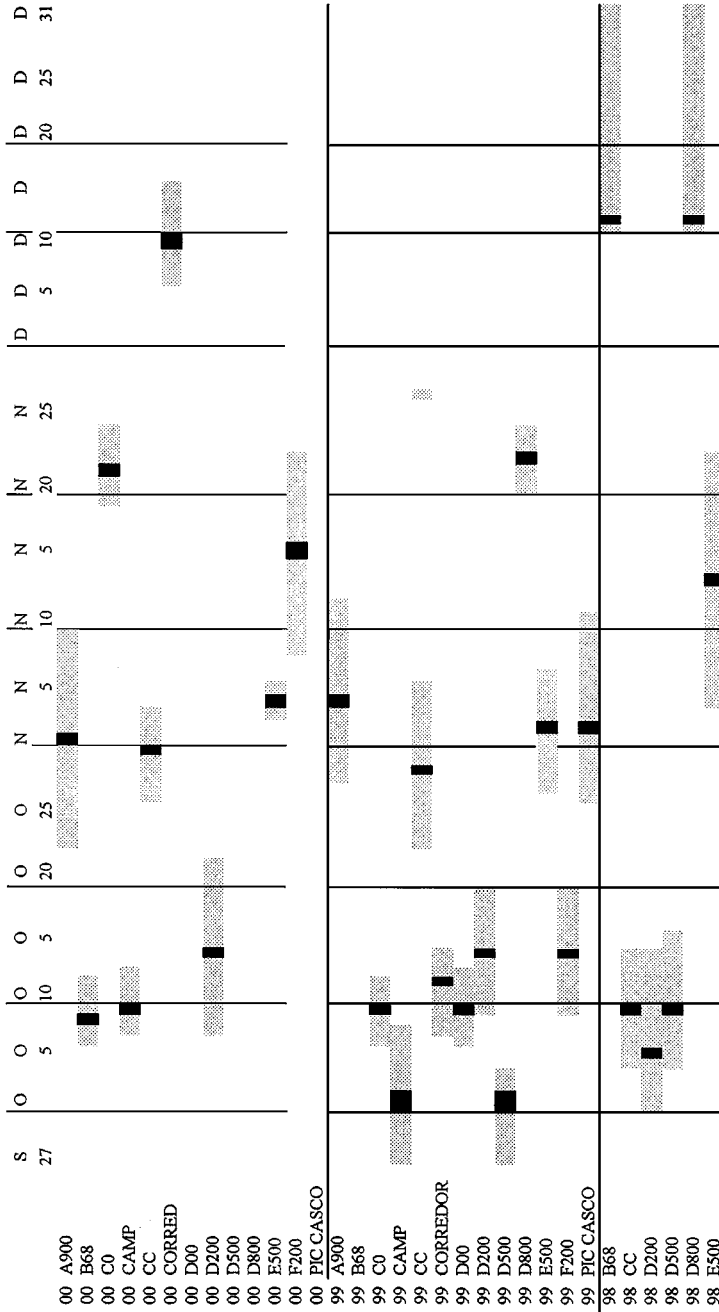
Fig. 2. Dates of birth (black boxes) and periods of birth (1998–2000, shaded bars).

(n = 13) occurred between September 27 and October 20; whereas another 11 occurred between late October and late November. Three births occurred during the last 3 weeks of December.

An analysis of the temporal distribution of the dates of birth uncovers a qualitatively different pattern (Fig. 2). There is one peak of births during the first 2 weeks in October (early season, 13 births), followed by a second peak during the first 2 weeks in November (mid-season, 11 births). Another 3 births occurred 2 weeks later (late season). Although timing of the early birth season seems to be constant year after year, there seems to be differences between years in the distribution of births through the season. During 2 years when groups were most intensively studied (1999–2000), 58% of births (7 of 12 births) occurred early in the season (1999), whereas only 33% (3 of 9) births occurred during the first 2 weeks in October, 2000.

As a consequence of the seasonal pattern of births, most interbirth intervals (IBIs) were remarkably close to one year (median: 370 days, range: 345–426, n = 13 intervals from ten groups, Table III). There is some indication that the timing of a birth in one year had a strong influence on the timing in the following year. Groups that did not have infants (n = 3 no recorded births) or had them in the early season (n = 9 births), had infants early (n = 7), late (n = 3) or not at all (n = 2) in the following year. Conversely, if groups had infants in the mid or late season (n = 7 births), they never gave birth in the early season of the following year. They either failed to produce infants

Table III. Dates of birth and interbirth intervals (in days)

	Dates of birth			Interbirth interval after	
Group ID	1998	1999	2000	Early birth	Mid/late birth
A900	NA	**04-Nov-99**	**1-Nov-00**		363
B68	**12-Dec-98**	NO	*8-Oct-00*		
C0	NO	*09-Oct-99*	**21-Nov-00**	409	
Camp	NA	*01-Oct-99*	*9-Oct-00*	374	
CC	*9-Oct-98*	**29-Oct-99**	**31-Oct-00**	385	368
Corredor	NA	*11-Oct-99*	**10-Dec-00**	426	
D100	NO	*09-Oct-99*	NO		
D1200	*5-Oct-98*	*14-Oct-99*	*14-Oct-00*	374,366	
D500	*9-Oct-98*	*01-Oct-99*	NO	357	
D800	**12-Dec-98**	**22-Nov-99**	NO		345
E500	**13-Nov-98**	**02-Nov-99**	**4-Nov-00**		354,368
F1200	NA	*14-Oct-99*	**15-Nov-00**	398	
Median (days)				380	371
Range				357–426	345–368

Note. Italic: early season births; Bold: mid and late season births. NA: the group was not regularly monitored to determine if a birth occurred or not. NO: group regularly monitored, but no birth recorded.

(n = 2) or had them in the mid or late season again (n = 5). In other words, a night monkey is more likely to have a birth early in the season following an early birth than following a mid or late birth (Fisher's Exact Test, n = 19, p = 0.017). These findings suggest that the length of the IBI is influenced by the timing of the preceding birth and that there may be a constraint to reduce the IBI to <1 yr. The IBI tends to be longer following a birth in the early season than one in the mid or late season (Wilcoxon Signed Ranked Test, z = −2.032, p = 0.042).

DISCUSSION

Our data show that there is a marked seasonal distribution of night monkey births in the gallery forests of Eastern Formosa, Argentina. We only recorded births between late September and mid-December, with almost 90% of them occurring in an 8-week period. The unusual pattern of diurnal and nocturnal activity of night monkeys in this region may be an adjustment to extreme environmental conditions (Fernandez-Duque *et al.*, 2001; Rotundo *et al.*, 2000).

We propose that the timing of mating behavior and births in the population may be heavily influenced by changes in photoperiod and ambient temperature. We hypothesize that shortening of photoperiod during April–May may activate the reproductive system of female night monkeys, which may enable them to conceive and begin pregnancy when they can avoid extremely high temperatures that could be metabolically challenging. Furthermore, the rains of April may provide an adequate food supply for newly-pregnant females.

In the Chaco, photoperiod is the only environmental factor that can be accurately predicted, even when infrequent climatological phenomena occur, e.g., El Niño and La Niña events. Thus, changes in day length may be the most reliable information to predict future conditions amenable for reproduction. Changes in day length during April and May indicate the end of extreme high temperatures. Beginning in April, temperatures above the potential thermoregulatory zone of night monkeys are rare if not altogether absent. There is ample evidence to show that temperatures above thermoneutrality negatively affect reproduction. The effects, which have been described in mice, rats, sheep and cattle (Bronson, 1989) seem to be present regardless of body size. The effects of high temperatures can also be acute in males because they suffer a direct action on the gonads (Bronson, 1989, p. 95).

It is possible that adequate ambient temperatures coupled with a reduction or absence of lactation allows females to resume cycling. The fact that we

never observed mating behavior before May supports this alternative. The timing of mating and conception determines the period when the birth and weaning of the infant will occur. From the infant perspective, it may be important to achieve full independence before very low temperatures become frequent. Although captive infants suckled when they were 16–18 weeks old (Dixson and Fleming, 1981) and we have seen ≥2 infants attached to the nipple when they were approximately 9 mo old, most infants forage and eat solids independently during the third or fourth month of life. Thus, infants born in October–November will have achieved total independence before the cold months of May–July.

Infant survival during the first 6 mo of life was high (96%, 26 of 27). The only female that lost her infant did not give birth again until the next birth season: the interbirth interval was not shortened by the death of the infant. This finding, coupled with information from captive studies suggesting the interbirth interval of night monkeys in captivity lasts on average 8 mo, is further evidence for a strong environmental influence on the timing of births (Dixson, 1983). Because it is possible that some of the groups recorded as having no infants had ones that died before we could notice them, we may have overestimated infant survival.

Additional evidence for the responsiveness of night monkey reproductive systems to changes in photoperiod comes from field studies conducted in the tropics. Where changes in photoperiod are less pronounced, free-ranging night monkeys show a smaller degree of birth seasonality than in Formosa. One field study conducted in southeastern Perú, showed that all 9 births in 4 groups of *Aotus nigriceps* occurred between August and February (Wright, 1985). *Aotus nancymaae* and *A. vociferans* give birth during a 3–4 mo period in Northeastern Perú (Aquino *et al.*, 1990).

Studies in captivity have also indicated that night monkey reproductive systems responds to changes in photoperiod. Tropical species (*Aotus lemurinus* and *A. nancymae*) bred through the year when photoperiod was kept constant (Dixson, 1994; Malaga *et al.*, 1997). Conversely, one of the species adjusted its reproduction when housed in the tropics under conditions of natural photoperiod. When *Aotus nancymaae* were bred in captivity (Center for Reproduction and Conservation of Non-Human Primates, Iquitos, Perú, 73° W, 4° S) with natural ambient temperature and photoperiod, half the births (66 of 126) occurred between October and January (Gozalo and Montoya, 1990). Similarly, in a colony of *Aotus vociferans* at the same location, 75% of births occurred between December and May, and more than half between December and March (Montoya *et al.*, 1995). A similar seasonal pattern, but shifted 6 mo, occurs at Monkey Jungle in Miami, Florida (Dumond Conservancy for Primates and Tropical Forests, Inc., 25° 50′N). When night monkeys, mainly *Aotus nancymaae*, that had

lived in indoor facilities in the USA, were housed in the outdoor subtropical environment with a distinct wet and dry season under natural lighting, they became more and more seasonal breeders the longer they lived outdoors (Evans, pers. com.). Most births in Monkey Jungle are confined to the March mid-November period, a 6-mo difference from the birth season in Formosa, which corresponds to the shift in seasons between hemispheres.

The birth seasonality of *Aotus azarai* in Formosa is comparable to the seasonality of some other primate species in areas where changes in temperature and photoperiod are also relatively extreme. Some prosimians of Madagascar have remarkable reproductive seasonality, related, at least in part, to the extreme environmental conditions of the forests they inhabit. Four of 5 groups of mongoose lemurs (*Eulemur mongoz*) gave birth during a one-week period in October (Curtis, 1997). Ring-tailed lemurs have a very restricted mating and breeding season (Jolly, 1966). For example, 27 of 29 births in two troops of *Lemur catta* occurred between September 18 and October 25 (Sauther, 1991, 1998). Sifakas are also seasonal breeders, giving birth during a restricted period that occurs mainly in June–July (Meyers and Wright, 1993). A comparative study of *Propithecus tattersali* and *P. diadema edwardsi* showed that although there is strict seasonality in both species, resource availability could not be the cause of it since they live in significantly different forests with different regimes of food availability (Meyers and Wright, 1993). In a comprehensive review of the breeding seasonality of 11 taxa of captive lemurs, Rasmussen (1985) modeled the way in which changes in photoperiod may trigger reproductive activity in lemurs. The timing of their reproductive events is very similar to the timing of reproduction in *Aotus azarai* in Formosa. Given that some of the lemurs live at exactly the same latitude as night monkeys, the finding provides further support for the role of photoperiod in regulating night monkey reproduction.

A comparison of Chaco night monkeys and lemurs provides further insight into the role of a harsh environment shaping the biology of night monkeys. Relatively low basal metabolic rate, small group sizes, breeding seasonality, and cathemerality are but a few of traits common to lemurs and *Aotus azarai*. Wright (1999) argued that in lemurs, many of these traits could be the result of selection favoring energy conservation in the harsh, unpredictable environment of Madagascar. An increase in size—Bergman's Rule—is associated with cold environments. Data on 10 night monkeys captured at our site suggest an adaptation to the harshness of low winter temperatures. The 4 adults weighted 1300, 1355, 1550, and 1580 g, whereas a 14-mo-old female weighted 910 g. The juvenile weight is within the range of adult weights reported for other *Aotus spp*. species, and the adult weights are almost 50% higher than their weights (Smith and Jungers, 1997).

Females will be selected to cue on changes in photoperiod as long as the strategy increases the number of offspring they produce. Unfortunately, with no long-term datum on the reproductive success of females breeding early or late or not breeding in certain years, the ultimate forces shaping birth seasonality are hypothetical. In a recent review of the ultimate factors favoring birth seasonality in Neotropical primates, Di Bitetti and Janson (2000) examined energy availability as a significant selective force. They evaluated whether birth seasonality is better explained for a particular taxon as a strategy to facilitate storing resources for future use, to reduce maternal energy stress by timing the energy-expensive period of lactation, or to reduce mortality of infants by timing the weaning period. Unfortunately, due to the lack of adequate data, *Aotus spp.* were not included in their analysis. They suggested that for a small-bodied genera that produce one offspring per year (like *Aotus*) it may be peak lactation rather than infant weaning that is being timed to overlap with maximum food availability.

Female *Aotus* may achieve a positive energetic balance to engage in a new reproductive event following a sudden abundance of fruits, coupled with milder temperatures. Once females were cycling in response to a change in photoperiod, it would be the availability of an adequate food supply that increases the probability of conception by allowing her the extra energy to endure pregnancy. During the last 20 years, April has been characterized by heavy rainfall. The heavy rains of April trigger the maturation of fruits of *Chryshophyllum gonocarpum* (Placci, 1995), which is highly preferred by night monkeys during May and June. Moreover, our data suggest that female lactation, occurs at a time when most tree species are producing fruits and insects are more abundant. Although the data strongly suggest that the abundance of flying insects changes throughout the year, it would be imprudent to speculate on the influence that the changes may have on the reproduction of night monkeys given the small number of samples collected and the significant daily fluctuations in insect abundance. Finally, the timing of births is such that it may reduce infant mortality since infants born in October–November can confront the low temperatures beginning in May as fully independent individuals.

In conclusion, our findings strongly support the idea of environmental control of reproduction in night monkeys. Interplay between changes in photoperiod and temperature may promote reproductive activity in females. Activation of mating during April–May–June may enable females to begin pregnancy at a time when the abundant rainfall triggers maturation of an important food source. Pregnancy occurs during a time void of extremely high temperatures that can be metabolically challenging. Lactation seems to be timed to a period of food abundance, whereas weaning occurs before the extreme low temperatures begin.

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