

Eduardo Fernandez-Duque

Influences of moonlight, ambient temperature, and food availability on the diurnal and nocturnal activity of owl monkeys (*Aotus azarai*)

Received: 4 October 2002 / Revised: 30 April 2003 / Accepted: 1 May 2003 / Published online: 7 August 2003
© Springer-Verlag 2003

Abstract The study of activity rhythms, their potential zeitgebers and masking factors among free-ranging primates has received relatively little attention in the past. Most primates are diurnal, a few of them nocturnal, and even fewer are cathemeral. Owl monkeys (*Aotus azarai azarai*) regularly show diurnal, as well as nocturnal, activity in the Argentinean and Paraguayan Chaco. The goal of this study was to examine how changes in activity patterns in owl monkeys of Formosa, Argentina are related to daily, monthly, and seasonal changes in temperature, light and food availability. During 1 year, I collected activity data from five groups followed continuously from dawn to dusk, dusk to dawn or uninterruptedly during 24 or 36 h for approximately 1,500 h. I kept hourly and daily records of temperature and light conditions, and I gathered monthly information on the density, distribution and abundance of food resources available to the monkeys. I found that the area of study is highly seasonal, and characterized by significant fluctuations in rainfall, temperature, photoperiod, and food availability. Owl monkeys had on average 5 h of activity during the day and 4 h during the night. The amount of diurnal activity remained fairly constant through the year despite seasonal changes in exogenous factors. Owl monkeys did not show changes in their activity patterns that could be attributed to changes in food availability. Nocturnal activity increased as the amount of moonlight increased, whereas diurnal activity decreased following a full-moon night. Ambient temperature was a good predictor of activity only when the moon was full. These results argue convincingly for an interaction between ambient temperature and moonlight in determining the observed activity pattern. It is then highly advisable that

any evaluation of diurnal activity in cathemeral animals be analyzed controlling for the possible effects of moonlight during the previous night.

Keywords Activity patterns · Primates · Cathemerality · *Aotus* · Monogamy

Introduction

The temporal organization of behavior has profound implications for the survival and reproduction of animals (Daan and Aschoff 1982). Every animal must allocate time to the different activities (i.e., time budgets), and must distribute temporally those activities during a 24-h cycle (i.e., activity patterns). Most mammals concentrate their activities during one of two periods, i.e., they are either “diurnal” or “nocturnal” (Ashby 1972). A third group of organisms tends to be crepuscular, showing bimodal activity peaks occurring during the light/dark transition periods at dawn and dusk. The most infrequent activity pattern is the one in which animals have several peaks of activity during a 24-h cycle, a pattern referred to as ultradian, polyphasic, or cathemeral (Tattersall 1987).

The species-specific pattern of activity results from the interaction of the animal’s endogenous rhythm, its entrainment mechanisms, and the masking effects of certain environmental cues. In mammals, the most common environmental cue that serves as a synchronizing or entrainment agent (“zeitgeber”) of the circadian system to the 24-h solar day is the alternation of light and darkness. Entrainment of the circadian system by this environmental cycle will determine the phase of the activity rhythm, i.e., the times of the day when the animal will be active. However, the temporal distribution of activity is not only dictated by the circadian system. Other environmental factors such as ambient temperature, light and food availability, and predation risk may have direct effects on the level of activity. This phenomenon, known as “masking” of circadian rhythmicity, is equally important in determining the temporal activity pattern of a

Communicated by P. Kappeler

E. Fernandez-Duque (✉)
Center for Reproduction of Endangered Species,
San Diego Zoo, P.O. Box 120551, San Diego,
CA 92112-0551, USA
e-mail: efdunque@sandiegozoo.org
Tel.: +1-619-7443370
Fax: +1-619-5573959

species (Marques and Waterhouse 1994; Mrosovsky 1999; Rietvedl et al. 1993). Until recently, the majority of research on circadian rhythm was conducted on laboratory species. The study of activity rhythms and their potential zeitgebers and masking factors among free-ranging mammals received relatively little attention in the past and it was not a central topic in behavioral ecology.

More recently, there have been several ecologically oriented studies of activity rhythms in wild mammals (Bartness and Albers 2000; Halle and Stenseth 2000). The goal has been to examine the timing of daily activities of individuals as adaptations to the specific environmental conditions surrounding them. For example, among strictly diurnal mammals, the activity of squirrels was found to be influenced by food quality and availability (Wauters 2000). The activity patterns of mustelids are closely correlated with body size—smaller species are primarily nocturnal, whereas the larger ones have a more diverse activity pattern probably because of reduced predation risk (Zielinski 2000). Although the understanding of the behavioral and ecological adaptations of mammals showing ultradian or polyphasic rhythms remains limited, studies of voles (Halle 2000; Halle and Stenseth 1994), shrews (Merritt and Vessey 2000), and primates (Andrews and Birkinshaw 1998; Colquhoun 1993; Curtis and Rasmussen 2002; Curtis et al. 1999; Donati et al. 2001; Overdorff 1996; Overdorff and Rasmussen 1995; van Schaik and Kappeler 1993; Warren and Crompton 1997) are already providing enough data to justify the recognition of the new field of chronocology as a subdiscipline that promises to bridge the existing gap between chronobiologists and behavioral ecologists (Halle and Stenseth 2000).

Most primates are diurnal, a few of them nocturnal, and even fewer are cathemeral (van Schaik and Kappeler 1996; Wright 1999). Although most owl monkey (*Aotus* spp.) species of Central and South America are mainly nocturnal, *Aotus azarai azarai* regularly shows diurnal, as well as nocturnal, activity in the Argentinean and Paraguayan Chaco (Arditi 1992; Fernandez-Duque et al. 2001; Rotundo et al. 2000; Wright 1985). The strictly nocturnal owl monkeys of Colombia (*A. lemurinus griseimembra*) have been the focus of a series of laboratory studies analyzing circadian rhythms of locomotor activity, as well as their entrainment and masking by light (Erkert 1976, 1991; Erkert and Grober 1986; Erkert and Thiemann-Jager 1983; Rappold and Erkert 1994; Rauth-Widmann et al. 1991). The cathemeral owl monkeys of the Argentinean Chaco provide an additional opportunity for examining some of the environmental factors possibly affecting the temporal organization of activity patterns in this small mammal.

In this study, I evaluated two hypotheses proposed to explain cathemerality in primates (Overdorff and Rasmussen 1995; van Schaik and Kappeler 1993; Wright 1989, 1999). One hypothesis suggests that cathemerality may result from unusually harsh climatic conditions, whereas the second one poses that cathemerality may be the consequence of a pronounced seasonality in resource

availability. If the extremely low and high temperatures characteristic of the Chaco pose a thermoregulatory challenge to owl monkeys, cathemeral activity may result from changes in the temporal organization of behavior to minimize thermoregulatory metabolic costs. Alternatively, cathemerality in owl monkeys may be causally linked to significant fluctuations in food availability that may pose an additional metabolic stress. When high-energy foods are scarce, owl monkeys may have to increase the amount of fibrous foods they eat (Ganzhorn and Wright 1994). Their lack of digestive specializations for folivory makes it necessary for them to minimize the time that fibrous food is not being processed. This is achieved by interspersing periods of processing and harvesting over a 24-h cycle, which results in an ultradian rhythm of activity. Thus, I predict that if cathemerality occurs mainly in response to changes in ambient temperature, owl monkeys will be strictly nocturnal when temperatures are high regardless of availability of high-energy resources. However, if cathemerality is, at least partially, a response to seasonal changes in food availability, owl monkeys will increase their diurnal activity during months in which the availability of fruit and insects is less regardless of climatic factors.

To evaluate the extent to which the diurnal activity of owl monkeys may be causally linked to the considerable variation in daily and seasonal temperatures characteristic of the Gran Chaco and the fluctuations in food availability, I asked the following questions: What is the extent of the diurnal and nocturnal activity of owl monkeys in Formosa, Argentina? Are there seasonal changes in their activity patterns? What are the proximate determinants that structure their circadian rhythm? What is the influence that the ambient temperature, the day/night cycle of illumination, the lunar phase and the availability of food have on the temporal organization of activity patterns in owl monkeys? To address these questions, I examined how the daily temporal distribution of activity of owl monkeys (*A. azarai azarai*) is affected by these exogenous factors in Formosa, Argentina.

Methods

Area and population of study

The area of study, which includes a mosaic of grasslands, savannas, dry and gallery forests, is located outside of the tropics (58°11'W, 25°58'S) at approximately 60 m above sea level. I mapped 70 ha of gallery forest to facilitate the location of the different groups of monkeys. Within those 70 ha, I established 14 km of transects, running east-west and north-south, and spaced every 100 m. I measured and marked transects every 50 m with fluorescent plastic flagging tape and aluminum tags. An 18-month study of the forest conducted 15 km upstream from the area of study provided a detailed description of forest structure (Brown et al. 1993).

The area of study is characterized by significant seasonal fluctuations in rainfall, temperature, and length of time between sunrise and sunset (Fernandez-Duque et al. 2002). Annual rainfall has averaged 1,555 mm between 1977 and 2000. Monthly average rainfall varies significantly during the year, with two rain peaks in April and November, and a relatively dry season lasting from June

Table 1 Seasonal changes in ambient temperature, daylength and rainfall in Guaycolec, Formosa, Argentina. Rainfall data are from the period 1977–2000, whereas temperature and photoperiod data were recorded between Aug. 1998 and Aug. 1999

Month	J	F	M	A	M	J	J	A	S	O	N	D
Monthly mean temp. (°C)	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
No. days with <i>T</i> max >33°C	22	20	18	0	0	0	0	0	4	11	17	18
No. days with <i>T</i> min <10°C	0	0	0	4	9	11	16	5	5	0	0	0
Day length (h)	15.4	14.7	13.9	13.2	12.6	12.3	12.4	12.9	13.6	14.4	15.2	15.7
Rainfall (mm±SD)	154±102	153±73	130±78	236±183	124±78	59±45	46±52	64±68	108±76	140±90	211±128	135±95

to August. Seasonal changes in temperature are also pronounced. During 1998–1999, monthly mean temperatures were on average 11°C lower during winter months (May–August 1998) than they were during summer months (December–March). Extreme low and high temperatures were also frequent. Daily minimum temperatures below 10°C occurred between April and September, whereas maximum daily temperatures above 33°C were concentrated between September and March (Table 1). The time between sunrise and sunset was more than 3 h longer during the summer (December–January), than it was during the winter months (June–July).

The gallery forests described above are home to the owl-monkey subspecies *A. azarai azarai*, which is found in the Argentinean provinces of Formosa and Chaco (Brown and Zunino 1994). The population of study includes 15 neighboring groups of owl monkeys that have been monitored in the cattle ranch “Estancia Guaycolec” since 1997 (Fernandez-Duque et al. 2001). The reproduction of owl monkeys at this relatively high latitude is extremely seasonal and heavily influenced by the particular environmental conditions of the Chaco. Matings have only been observed between May and September, whereas births occur between late September and mid-December.

Data collection

Insect abundance, phenology and rainfall data

Owl monkeys have been reported to eat insects (Wright 1985). I obtained data on the availability of insects using light-traps (Smythe 1997). A light-trap consists of a light source, a collecting cone, and a bag filled with poison. I left two light-traps on all night (1800–0600 hours), on average twice a month. I collected 58 samples on 40 nights between 20 August 1998 and 17 August 1999. I have presented elsewhere a more detailed description of how I evaluated seasonal changes of the availability of insects (Fernandez-Duque et al. 2002).

To evaluate relative changes in the density, distribution, and abundance of plant resources, I collected monthly information on forest composition and phenology from 30 plots (50×10 m) placed randomly in approximately 30 ha of forest. I sampled a total of 1.5 ha, representing 5% of the total area used by the five monkey groups being studied.

I obtained monthly rainfall data for the period 1977–1999 from records kept at Estancia Guaycolec.

Temperature and light-intensity data

I recorded temperature hourly using a Stowaway XTI temperature automatic data logger between 11 August 1998 and 16 August 1999.

To estimate available light during the day, as well as during the night, I used a Stowaway light-intensity logger with the sensor directed towards the zenith. It is a general-purpose light-intensity

logger with recording intensities from 0.1 to 10,000 lx. The data logger recorded light intensity every 15 min during 1 year (11 August 1998 to 10 August 1999).

I define nocturnal activity as activity occurring during the nautical night. Nautical night is the time period defined as beginning and ending when the sun is geometrically 12 degrees below the horizon. Diurnal activity includes activity occurring between local sunrise and sunset and activity taking place during nautical dusk and dawn. The duration of twilight before sunrise (“dawn”) was calculated as the time between the first data-logger record and the time when the sun appeared in the horizon as obtained from astronomical tables. The duration of twilight after sunset (“dusk”) was similarly obtained, using the time the sun disappeared in the horizon and the last record of the logger.

Behavioral data

Five neighboring groups (C0, Cola Corta, D100, D500, E500), which were very well habituated to humans and had been observed since 1997 (Fernandez-Duque et al. 2001), were the focus of behavioral observations. I observed the groups during approximately 1,500 h between August 1998 and September 1999. I collected data during complete diurnal follows that began at dawn and finished at dusk (“12D”, *N*=87 follows), and nocturnal follows that began at dusk and finished at dawn (“12N”, *N*=38). I did some of the diurnal and nocturnal follows consecutively, resulting in 24-h follows (“24”, *N*=12). On five occasions, I followed the monkeys continuously for 36 h (D100, *N*=4, C0, *N*=1). For the analyses presented below, I discarded four nocturnal follows for various reasons that affected the quality of the data substantially (e.g., long times without contacting the group, confusion between neighboring groups). Table 2 summarizes the annual distribution of diurnal and nocturnal follows conducted for each group.

Despite my efforts, I was not able to sample evenly through the different months, temperatures, and moon phases. For example, I sampled diurnal activity more than twice as much as nocturnal activity (87 vs 38 follows) because of the difficulties inherent to working at night. One group (D100) was sampled almost twice as much (*N*=39 follows) as the others (C0, CC, D500, and E500 followed 25, 22, 18, and 13 times, respectively). Finally, it was not possible to completely balance the sampling of each group during each moon phase. Whenever appropriate, I discuss the possible influence of sampling effects on the results.

The sampling schedule was extremely intensive even when considering the sampling limitations described above. Such an intense sampling schedule of a cathemeral, tree-dwelling small primate was only possible with the collaboration of a large number of observers. During the study, 15 different observers of various backgrounds and training collaborated in data collection. Observers were organized in teams of two or three people, including at least one experienced observer (i.e., someone who had had several months of experience working with the animals). One observer was responsible for maintaining eye-contact with as many members of the group as possible, whereas the second observer was responsible

Table 2 Number of monthly complete day and night follows of each group

Group name	Month												Total follows per group
	J	F	M	A	M	J	J	A	S	O	N	D	
Day follows													
C0	3	1	1	1	1	2	2	5	1	1		1	19
CC	3		2		1	3	3	1		2	2		17
D100	1	1		5	7	5	1	2	1		1	1	25
D500	1	1	1		1	1	4	1	1		2	2	15
E500	3		1	1		1	1	2	1		1		11
Total follows per month	11	3	5	7	10	12	11	11	4	3	6	4	87
Night follows													
C0	1	1				1		2	1	1			7
CC	3					1	1				1		6
D100	1	1		2	4	6			1				15
D500		3								1	1	1	6
E500	2		1						1				4
Total follows per month	7	5	1	2	4	8	1	2	3	2	2	1	38

for writing down the observations on a check-sheet. In the analysis presented here, I minimized the potential problems of inter-observer reliability by assigning all behavioral records to one of two exclusive categories: active/inactive, these categories being the simplest to differentiate (see below).

We collected data during 10-min observation periods conducted three times per hour (min 0–10, min 20–30, min 40–50). It was not feasible to conduct observations of specific individuals at day and night in a comparable manner. Therefore, observations were not made of a specific individual, but instead, the focus of the observation was the group. We observed the animals with binoculars or the naked eye during daylight and with a pair of night-vision binoculars during the night (ITT, Gen III). During any 10-min observation period, we recorded the activity state (foraging, moving, or resting) of all visible animals every 2 min. The relatively small group size (three to six individuals) made it possible to record the behavior of most animals in the group at each sampling point. For the analyses presented here, I summarized the data into two exclusive categories: active (moving or foraging) or inactive (resting). At each of the five sampling points in a 10-min focal, I gave a score of “Active” or “Inactive” to the whole group based on the data collected for each of the visible animals. Most of the time, the high synchronicity of behaviors among individuals in the group made the decision unequivocal since all animals had been recorded as doing the same (e.g., all of them scored for Resting). Whenever different animals were involved in different activities, the group was considered Active or Inactive based on what the majority of individuals were doing.

Data analysis

I estimated insect abundance by obtaining a monthly mean of dry weight for all the samples collected during any given month. Then, I evaluated monthly changes using the Kruskal Wallis test. The analysis of seasonal changes in plant food abundance is based on phenology data I collected from 30 different tree species ($N=750$ trees). I obtained the percentage of species showing each phenophase at any particular month (presence or absence of phenophase) for each of the three observers; then I obtained a monthly mean. I analyzed the monthly changes using the Friedman test for several related samples. I present the monthly rainfall data to illustrate the seasonal aspect of the area, but no analyses are presented using rainfall as a predictor of activity.

For each day, I summarized the temperature data using the 24 hourly temperature records obtained per day. For each 24-h period, I calculated the following temperature parameters: minimum,

maximum, range, and mean temperature. Using daily values, I computed monthly means of all parameters. A stepwise regression analysis on mean, minimum, maximum, and daily temperature range indicated that the maximum temperature of the day was the best predictor of activity during the light or the dark phase of the light/day cycle. Thus, the association between temperature and activity was evaluated using maximum temperature as the independent variable.

For the analysis of the effects of moonlight on activity, I used four categories corresponding to new moon and full moon and two categories for intermediate phases of the moon based on the percentage of moon surface illuminated. I considered new-moon nights those with less than 10% of the moon illuminated, and full-moon nights those with more than 89% of the moon illuminated. The two intermediate fractions had 10–49% and 50–89% of the moon illuminated.

The amount of nocturnal and diurnal activity was analyzed based on the number of sampling points when the group was active or inactive. For simplicity, figures and tables present data as mean number of hours, based on the number of 2-min intervals during which activity or inactivity were recorded. A total count of sampling points when the group was active was obtained for each follow and a mean computed for each group. Then an estimate of time in hours was obtained. For example, if a group was followed from 0700 to 1900 hours, there would be 180 sampling points (12 h \times 3 observation periods per hour \times 5 sampling points per observation period). If on 90 of those sampling points, I scored activity, then I say that the group spent 6 h of the time active. In other words, whenever used, “time” or “hours of activity” refer to the number of 2-min sampling points, not actual duration of the bout of activity or inactivity.

The non-parametric Wilcoxon Signed Ranked test for two unrelated samples was used to evaluate differences in the availability of insects, and the Friedman test to evaluate differences in the total amount of nocturnal and diurnal activity among groups ($N=5$ groups). A one-way analysis of variance was used to evaluate differences in the amount of diurnal and nocturnal activity across the year, as well as to evaluate differences in the effects that moonlight had on diurnal activity during the following day.

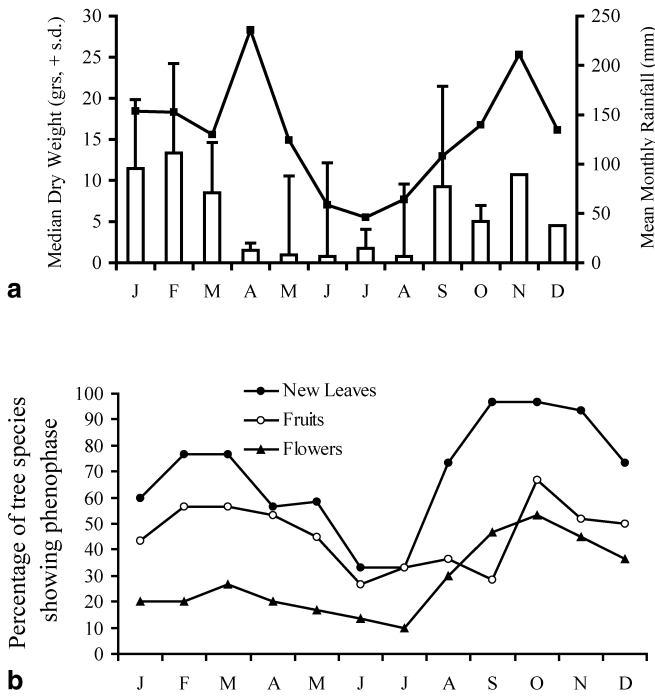


Fig. 1 **a** Monthly medians of dry weight of captured insects \pm SD (bars) and monthly means of rainfall during 1977–1999 in Estancia Guaycolec, Formosa (curve). **b** Seasonal changes in the percentage of tree species showing new leaves, fruits, and flowers. Percentages are based on the total number of tree species monitored monthly (30 species)

Results

Effects of seasonal factors

The study area is highly seasonal, characterized by significant fluctuations in rainfall, temperature, and photoperiod (Table 1). The relative abundance of available food also changed significantly through the year. The weight of captured insects was considerably higher between September–March than it was between April–August (Wilcoxon, $z = -3.139$, $p = 0.002$, Fig. 1a). A considerable degree of seasonality in the availability of new leaves, fruits, and flowers was also detected (Fig. 1b). The percentage of tree species producing fruits, flowers, or new leaves varied significantly through the year (fruits: $\chi^2 = 18.00$, $df = 11$, $p = 0.081$; flowers: $\chi^2 = 51.49$, $df = 11$, $p < 0.001$; new leaves: $\chi^2 = 178.26$, $df = 11$, $p < 0.001$), reaching a low in the coldest and driest months of June and July. For example, only 27% of tree species produced fruits during June (8 of 30 spp., Fig. 1b). However, a higher percentage of species produced fruits, flowers, and new leaves beginning in September. For example, 67% of tree species were recorded with fruits in October (20 of 30 species).

Owl monkeys were active during the day, as well as during the night. They had on average 5 h of activity during the day and 4 h during the night (Fig. 2). Approximately one-quarter of the time spent active

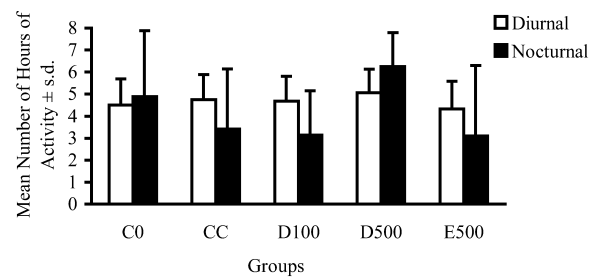


Fig. 2 Mean number (\pm SD) of hours of nocturnal and diurnal activity for each of the five studied groups

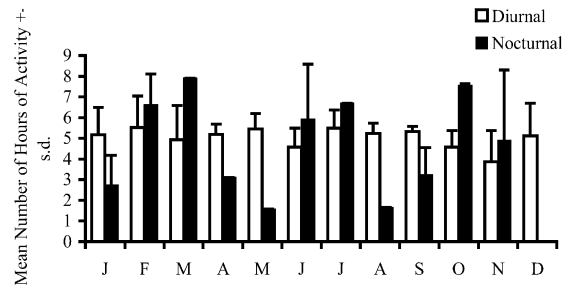


Fig. 3 Monthly changes in mean number of hours of diurnal and nocturnal activity. No data are available for nocturnal activity in December (D). Each column represents the grand mean obtained from averaging the means of all groups sampled in each month

during the day took place during twilight. The total combined time spent active during the morning and evening twilight was on average 1.3 ± 0.5 h. During only one of the follows, did I not record activity at this time of the day. Differences among groups in the amount of nocturnal or diurnal activity were not statistically significant (Friedman: nocturnal: $\chi^2 = 6.66$, $df = 4$, $p = 0.154$; diurnal: $\chi^2 = 5.65$, $df = 4$, $p = 0.226$). Because there were no significant differences in the amount of diurnal and nocturnal activity among groups, the data were combined for the analysis of the effects of light and temperature.

The amount of time the monkeys spent active during the light phase of the light/dark cycle did not change much through the year (Fig. 3). Still, because daylength changed significantly during the year (Table 1), this relatively constant number of hours of diurnal activity means that the groups were active a significantly higher percentage of the light phase of the light/dark cycle during certain months. Groups spent on average 42% of the light-phase hours active between May and September, whereas they were active only 34% of the time between October and April. Neither the number of hours of diurnal activity changed significantly through the year as indicated by a one-way analysis of variance ($F_{11,33} = 0.707$, $p = 0.723$), nor was the percentage of hours of diurnal activity statistically significant ($F_{11,33} = 1.698$, $p = 0.117$). Although the data as depicted in Fig. 3 may suggest that monthly changes in nocturnal activity were much more pronounced, most changes can be explained by the effects of the moon on nocturnal activity (see below).

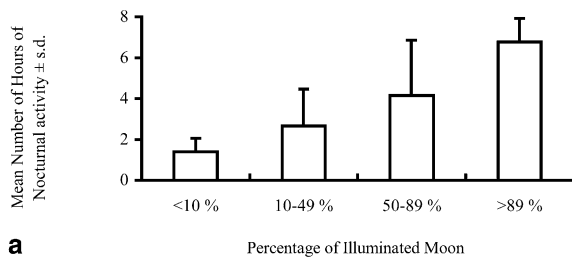
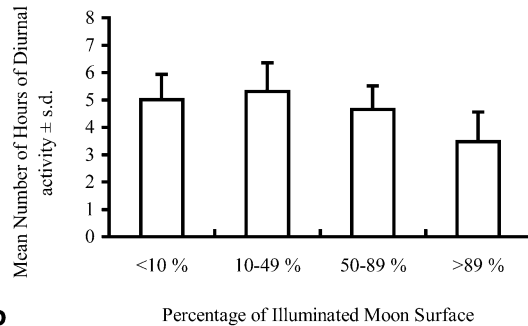
**a****b**

Fig. 4a, b Changes in the mean number of hours of nocturnal (**a**) and diurnal (**b**) activity with changes in the percentage of illuminated moon surface during the night or during the previous night (<10% new moon, >89% full moon, 10–49% and 50–89% correspond to waning and waxing moon)

Table 3 Results of regression analyses tests showing the positive relationship between nocturnal activity and available moonlight for each group

Group	R^2	df	F	p	b_0	b_1
C0	0.92	5	58	0.001	6.3	70.5
CC	0.50	4	4	0.118	8.8	38.7
D100	0.57	12	16	0.002	2.1	44.3
D500	0.95	1	17	0.151	37.6	44.4
E500	0.99	2	187	0.005	14.2	64.3
Overall	0.57	32	43	<0.001	7.7	51.6

Effects of moonlight

The effects of moonlight were very pronounced on nocturnal, as well as diurnal, activity. Nocturnal activity increased as the amount of moonlight increased. All five groups tended to increase the amount of nocturnal activity as the illuminated fraction of the moon increased (Fig. 4a). When more than 90% of the moon was illuminated (i.e., full moon), nocturnal activity tended to be maximal and groups spent as much as 7 h of the night active. However, when the moon was not full, nocturnal activity ranged between 1.4 and 4.1 h. The relationship between nocturnal activity and moonlight was statistically significant for all 34 follows combined, as well as for 2 groups that were followed at least 5 times during the night (Table 3). A third group showed a positive relationship that fell short of statistical significance. The remaining two groups also showed a statistically significant positive relationship, but the statistical outcomes are meaningless

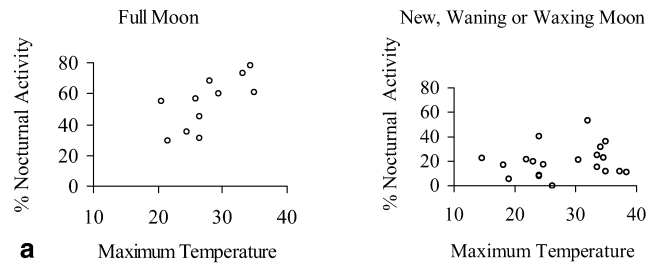
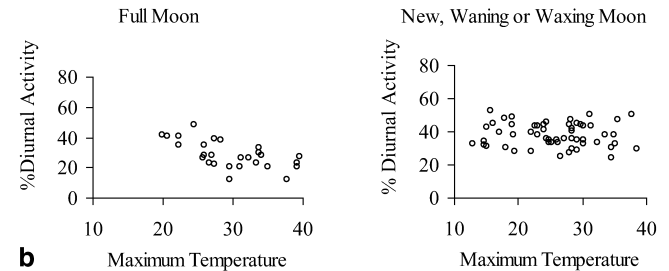
**a****b**

Fig. 5a, b Relationship between hours of nocturnal and diurnal activity and maximum temperature

given the small number of follows conducted on each of those groups ($N=3$ or 4 follows).

Diurnal activity was also influenced by the amount of moonlight during the previous night. Groups showed less diurnal activity following a full-moon night than they did after a night when the moon was only partially illuminated (ANOVA: $F_{3,79}=9.406$, $p<0.001$, Fig. 4b).

Effects of ambient temperature

Ambient temperature was a good predictor of nocturnal activity only when the moon was full. During nights of full moon, the level of nocturnal activity could be predicted by the maximum temperature reached during that day. The groups showed more nocturnal activity following a day of very high temperatures than they did after a relatively cool day. A linear regression analysis indicated that the positive relationship between the number of hours of nocturnal activity and maximum temperature was not statistically significant (adj. $R^2=0.217$, $t=1.825$, $p=0.093$), whereas the relationship between the percentage of night hours and maximum temperature was statistically significant (adj. $R^2=0.393$, $t=2.786$, $p=0.016$, Fig. 5a). However, when the moon was new, waning, or waxing, the groups were generally inactive regardless of temperature. Maximum temperature was not a good predictor of the general level of nocturnal activity, either measured as the total number of hours (adj. $R^2=0.005$, $t=0.291$, $p=0.774$) or the percentage of night hours (adj. $R^2=0.029$, $t=0.928$, $p=0.366$).

The relationship between ambient temperature and diurnal activity also depended on the moonlight available during the previous night. Following a full-moon night,

the groups showed less diurnal activity as the temperature increased. A linear regression analysis indicated that the decrease in the percentage of diurnal activity with an increase in maximum temperature was significant (adj. $R^2=0.387$, $t=-3.975$, $p=0.001$, Fig. 5b). When the moon was new, waning, or waxing, ambient temperature was not correlated with the total amount of diurnal activity. Groups did not change the amount of diurnal activity as maximum temperature increased, as indicated by the lack of a significant positive relationship between percentage of diurnal activity and maximum temperature (adj. $R^2=0.066$, $t=-0.483$, $p=0.631$, Fig. 5b).

Discussion

Owl monkeys in Estancia Guaycolec showed both diurnal and nocturnal activity. This cathemeral activity is in good agreement with previous reports of owl monkeys in the same area of study, as well as from a population in the Paraguayan Chaco (Arditi 1992; Fernandez-Duque and Bravo 1997; Rotundo et al. 2000; Wright 1989). However, it was unexpected to find that they were as active during the light phase as they were during the dark phase of the 24-h cycle.

Other populations of *A. a. azarai* at lower latitudes and populations of the subspecies *A. azarai boliviensis*, also show some diurnal activity. Researchers conducting surveys of primates encountered active owl monkeys during daylight work in Paraguay (Brooks 1996; Stallings et al. 1989), Bolivia (Mann 1956; Wallace et al. 1998), and Brazil (Fernandes 1993). García and Braza (1987) studied *A. azarai boliviensis* in Bolivia, but did not report diurnal activity. Instead, they reported that the first signs of activity took place 10–15 min after sunset, whereas activity stopped 10–20 min before sunrise. It is possible that diurnal activity was reduced during their study because they conducted the study exclusively during nights of full moon (see below). Systematic studies of activity patterns in other populations of *A. azarai* or other *Aotus* species are needed to understand whether the extent of diurnality in our population is a local response to particular environmental conditions or a trait common to other populations or species.

Owl monkeys in our population spent an average of 4 h active at night. *A. azarai* showed nocturnal activity that resembled what has been reported for other owl-monkey species that are strictly nocturnal. *A. nigriceps* in Manú National Park in Perú spent approximately half of the night active (Wright 1985; Fig. 14). A group of *A. azarai boliviensis* in El Beni in Bolivia spent approximately 50% of the time active during nights of full moon (García and Braza 1987), which results in a similar number of hours of activity as we observed during full-moon nights.

The total amount of diurnal activity remained fairly constant through the year despite the seasonal changes in food availability, temperature, and rainfall. The environment where owl monkeys live in the Argentinean Gran Chaco shows a relatively high degree of seasonality in

climate and food abundance. Mean monthly temperatures were notably different at different times of the year and marked differences in temperature occurred daily (Fernandez-Duque et al. 2002). The seasonal pattern of rainfall and temperature in Formosa correlated with changes in fruit, flower, and new leaf production. If cathemerality in owl monkeys were, at least partially, a response to food availability and digestive constraints as has been hypothesized (Engqvist and Richard 1991; Ganzhorn and Wright 1994; Overdorff and Rasmussen 1995), I would expect more diurnal activity during months of less fruit and insect availability. Owl monkeys did not show changes in their activity patterns that could be interpreted that way. Seasonal changes in activity patterns have been reported for various other primate species (Andrews and Birkinshaw 1998; Colquhoun 1993; Morland 1993; Wright 1999), as well as for a vast array of mammal taxa (Halle and Stenseth 2000). Following seasonal changes in food availability and rainfall, some species apparently switch from being mainly diurnal to being nocturnal, whereas others changed from diurnality to being active around the clock (Curtis 1997; Curtis and Rasmussen 2002). I was not able to analyze seasonal changes in nocturnal activity due to the smaller nocturnal sampling effort and the overriding effects of moonlight on nocturnal activity.

However, the data at hand provide convincing evidence for the influence that changes in moonlight and ambient temperature have on the activity patterns of owl monkeys. Nocturnal activity was strongly influenced by available moonlight. Nocturnal activity was maximum when more than 90% of the moon surface was illuminated. Then, owl monkeys spent most of the night active. However, nocturnal activity was minimal during nights of new moon. These findings are in total agreement with those reported for *A. lemurinus* in Colombia where owl monkeys showed marked lunar periodic variations in activity patterns under natural lighting conditions (Erkert 1974, 1976). Researchers in Peru and Bolivia have also reported intensive nocturnal activity during nights of full moon (Aquino and Encarnación 1986; García and Braza 1987; Wright 1978, 1989). Erkert replicated the patterns observed under natural lighting conditions in Colombia successfully in the controlled setting of the laboratory (Erkert and Grober 1986; Erkert and Thiemann-Jager 1983). When he simulated new-moon conditions by means of continuous low-light intensity, he observed suppression of the locomotor activity, indicating that low-light intensities or brightness changes during the dark phase caused particularly strong masking of the light/dark-entrained circadian activity rhythm. The strong negative masking effect of low-light intensity on the circadian rhythm of owl monkeys has also been observed in prosimians. Studies in captivity and in the field have demonstrated that red-fronted lemurs (*Eulemur fulvus rufus*) also require a certain luminosity threshold and below that threshold, activity is reduced (Donati et al. 2001; Erkert 1989). Red-fronted lemurs slowed down in the absence of moonlight and it is possible that the

absence of a tapetum lucidum in the species renders activity in total darkness difficult.

Quite unexpectedly, the effects of moonlight on the activity levels of owl monkeys persisted during the following light phase of the 24-h cycle. So, the amount of diurnal activity was negatively correlated with the available moonlight on the previous night. During a full-moon night, the animals were extremely active satisfying most of their social and digestive requirements. Once those requirements were satisfied, there was probably less need to be active during the following morning. However, following a night without moonlight, they needed to forage during daylight, which resulted in a relatively higher level of diurnal activity. This finding and the characteristic daily changes in temperature of the Chaco and some Madagascar habitats undoubtedly show the importance of evaluating diurnal and nocturnal activity under controlled moonlight conditions before conclusions can be reached about seasonal patterns (see also Overdorff and Rasmussen 1995).

Ambient temperature has long been recognized as an important environmental factor influencing activity patterns in mammals (Bartness and Albers 2000; Erkert 2000; Halle 1995; Perrigo 1987, 1990). Owl monkeys adjusted their periods of activity to changes in ambient temperature, but the effects of temperature were contingent on moon phase. Both nocturnal and diurnal activity were affected by temperature when the moon was full, whereas no effect of temperature was detected when less than 90% of the moon was illuminated. Owl monkeys apparently have a very narrow thermoneutral zone that may range between 28 and 30°C, and a relatively low resting metabolic rate (Le Maho et al. 1981; Morrison and Simoes 1962). In captivity, *A. lemurinus* was most active when the ambient temperature was 20°C and least active when it was 30°C (Erkert 1991). However, the existing characterization of the thermoneutral zone and the relatively low basal metabolic rate should be interpreted with special attention given to the geographic origins of the specimens studied, in view of the various activity patterns observed in the genus.

There are several other ecological and social factors that have been described as influencing activity patterns in mammals. Several small mammals are known to time their activities to minimize the risk of predation (e.g., Daly et al. 2000), and it is reasonable that the risk of predation may be influencing the activity patterns of owl monkeys as well. Wright (1989) hypothesized that predation pressure and competition for resources, two important selective forces that favor nocturnality in *A. trivirgatus* in Peru, are absent where cathemeral owl monkeys range. In the absence of dangerous diurnal raptors (e.g., harpy eagle), as well as other diurnal monkey species that compete for resources, the advantages of nocturnality for *A. azarai* may be limited. An incomplete adaptation to a nocturnal niche results in a cathemeral pattern of activity. Unfortunately, we lack any adequate data to test the influence of predators on owl-monkey activity patterns. Over the course of the years, I

have witnessed two attacks by raptors (*Pulsatrix perspicillata* and *Accipiter bicolor*) on groups of owl monkeys that occurred at dawn and dusk when owl monkeys tended to be most active. Somewhat anecdotal evidence from El Beni, Bolivia runs counter to the hypothesis that the absence of large diurnal raptors favors cathemerality in owl monkeys. At El Beni, where harpy eagles are present, owl monkeys showed diurnal activity when the climate was unusually cold (Mann 1956).

In conclusion, I found that the owl monkeys of the Argentinean Chaco are cathemeral, showing as much activity during the light phase as they did during the dark phase of the 24-h cycle. The total number of hours of diurnal and nocturnal activity remained relatively unchanged through the year, despite profound seasonal changes in rainfall, temperature, and food availability. Moonlight heavily influenced nocturnal and diurnal activity, whereas temperature effects were only detectable when the moon was highly illuminated.

These data argue convincingly for the importance of evaluating the potential interactions among various environmental factors in determining an observed activity pattern. For example, my data underscore the importance of evaluating seasonal changes in activity patterns with a very intensive year-round sampling that takes into account, not only monthly or seasonal changes, but daily or weekly changes as well (Overdorff and Rasmussen 1995). Moreover, given the important effects that full-moon nights may have on diurnal activity on the following day, it is imperative that diurnal and nocturnal sampling be conducted consecutively before conclusions can be reached about seasonal patterns.

Acknowledgements This research was supported by grants to E.F.D. from the L.S.B Leakey Foundation, the Douroucouli Foundation, Dumond Conservancy for Primates and Tropical Forests, and the Argentinean National Council for Scientific and Technological Research (PIP 0051/98, CONICET). I want to thank each of the volunteers and students who made this research possible by spending long hours in the forest: Suzanne Bartholf, Luciano Chaneton, Santiago De Paoli, Kate Maurer, Patricio Ramirez-Llorens, Marcelo Rotundo, Ana Sallenave, Carrie Sloan, Charles Veitch, Emilio White, Gustavo Zurita, as well as all of the Earthwatch and University of California Research Expedition volunteers who collaborated during the preliminary stages of this work. Special thanks go to the managers of Estancia Guaycolec, Mr. Emilio Arauz and Mr. John Adams for their continuous support. I thank Debbie Curtis and Claudia R. Valeggia, for their useful comments on the manuscript. Special gratitude is due to Hans G. Erkert and Horacio de la Iglesia who contributed their vast experience on chronobiology to improve substantially the quality of the manuscript. E.F.D. wrote this manuscript while a Postdoctoral Millennium Fellow at the Center for Reproduction of Endangered Species (Zoological Society of San Diego) and an Assistant Researcher at the CECOAL (Corrientes, Argentina). This study was conducted with full compliance of the current laws of Argentina.

References

- Andrews JR, Birkinshaw CR (1998) A comparison between the daytime and night-time diet, activity and feeding height of the black lemur, *Eulemur macaco* (Primates: Lemnidae), in Lokobe Forest, Madagascar. *Folia Primatol* 69:175–182

- Aquino R, Encarnación F (1986) Characteristics and use of sleeping sites in *Aotus* (Cebidae: Primates) in the Amazon Lowlands of Peru. *Am J Primatol* 11:319–331
- Arditi SI (1992) Variaciones Estacionales en la Actividad y Dieta de *Aotus azarai* y *Alouatta caraya* en Formosa, Argentina. *Bol Primatol Latinoam* 3:11–30
- Ashby KR (1972) Patterns of daily activity in mammals. *Mammal Rev* 1:171–185
- Bartness TJ, Albers EH (2000) Activity patterns and the biological clock in mammals. In: Halle S, Stenseth NC (eds) *Activity patterns in small mammals. An ecological approach*. Springer, Berlin Heidelberg New York, pp 23–47
- Brooks DM (1996) Some observations of primates in Paraguay. *Neotrop Primates* 4
- Brown AD, Zunino GE (1994) Hábitat, Densidad y Problemas de Conservación de los Primates en Argentina. *Vida Silvest Neotrop* 3:30–40
- Brown AD, Placci LG, Grau NR (1993) Ecología y Diversidad de las Selvas Subtropicales de la Argentina. In: Goin F, Goni R (eds) *Elementos de Política Ambiental*. Di Giovanni Grafica, La Plata, pp 215–222
- Colquhoun IC (1993) The socioecology of *Eulemur macaco*: a preliminary report. In: Kappeler PM, Ganzhorn JU (eds) *Lemur social systems and their ecological basis*. Plenum, New York, pp 11–23
- Curtis DJ (1997) Social structure and seasonal variation in the behaviour of *Eulemur mongoz*. *Folia Primatol* 70:79–96
- Curtis DJ, Rasmussen MA (2002) Cathemerality in lemurs. *Evol Anthropol* 1 [Suppl]:83–86
- Curtis DJ, Zaramody A, Martin RD (1999) Cathemerality in the mongoose lemur, *Eulemur mongoz*. *Am J Primatol* 47:279–298
- Daan S, Aschoff J (1982) Circadian contributions to survival. In: Aschoff J, Daan S, Groos G (eds) *Vertebrate circadian systems. Structure and physiology*. Springer, Berlin Heidelberg New York, pp 305–321
- Daly M, Behrends PR, Wilson MI (2000) Activity patterns of kangaroo rats. Granivores in a desert habitat. In: Halle S, Stenseth NC (eds) *Activity patterns in small mammals*. Springer, Berlin Heidelberg New York, pp 145–158
- Donati G, Lunardini A, Kappeler PM, Borgognini Tarli SM (2001) Nocturnal activity in the cathemeral red-fronted lemur (*Eulemur fulvus rufus*), with observations during a lunar eclipse. *Am J Primatol* 53:69–78
- Engqvist A, Richard A (1991) Diet as a possible determinant of cathemeral activity patterns in primates. *Folia Primatol* 57:169–172
- Erkert HG (1974) Der einfluss des mondlichtes auf die aktivitäts-periodik nachtaktiver saugtiere. *Oecologia* 14:269–287
- Erkert HG (1976) Lunarperiodic variation of the phase-angle difference in nocturnal animals under natural zeitgeber-conditions near the Equator. *Int J Chronobiol* 4:125–138
- Erkert HG (1989) Lighting requirements of nocturnal primates in captivity: a chronobiological approach. *Zool Biol* 8:179–191
- Erkert HG (1991) Influence of ambient temperature on circadian rhythms in Colombian owl monkeys, *Aotus lemurinus griseimembra*. In: Akivoshi E et al. (eds) *Primateology today*. Elsevier, Amsterdam, pp 435–438
- Erkert HG (2000) Bats. Flying nocturnal mammals. In: Halle S, Stenseth NC (eds) *Activity patterns in small mammals*. Springer, Berlin Heidelberg New York, pp 253–272
- Erkert HG, Grober J (1986) Direct modulation of activity and body temperature of owl monkeys (*Aotus lemurinus griseimembra*) by low light intensities. *Folia Primatol* 47:171–188
- Erkert HG, Thiemann-Jager A (1983) Dark switch in the entrainment of circadian activity rhythms in night monkeys, *Aotus trivirgatus* Humboldt. *Comp Biochem Physiol* 74A:307–310
- Fernandes MEB (1993) New field records of night monkeys, genus *Aotus*, in northern Brazil. *Neotrop Primates* 1:6–7
- Fernandez-Duque E, Bravo S (1997) Population genetics and conservation of owl monkeys (*Aotus azarai*) in Argentina: a promising field site. *Neotrop Primates* 5:48–50
- Fernandez-Duque E, Rotundo M, Sloan C (2001) Density and population structure of owl monkeys (*Aotus azarai*) in the Argentinean Chaco. *Am J Primatol* 53:99–108
- Fernandez-Duque E, Rotundo M, Ramírez-Llorens P (2002) Environmental determinants of birth seasonality in owl monkeys (*Aotus azarai*) of the Argentinean Chaco. *Int J Primatol* 23:639–656
- Ganzhorn JU, Wright PC (1994) Temporal patterns in primate leaf eating: the possible role of leaf chemistry. *Folia Primatol* 63:203–208
- García JE, Braza F (1987) Activity rhythms and use of space of a group of *Aotus azarai* in Bolivia during the rainy season. *Primates* 28:337–342
- Halle S (1995) Effect of extrinsic factors on activity of root voles, *Microtus oeconomus*. *J Mammal* 76:88–99
- Halle S (2000) Voles—small graminivores with polyphasic patterns. In: Halle S, Stenseth NC (eds) *Activity patterns in small mammals. An ecological approach*. Springer, Berlin Heidelberg New York, pp 191–215
- Halle S, Stenseth NC (1994) Microtine ultradian rhythm of activity: an evaluation of different hypotheses on the triggering mechanisms. *Mammal Rev* 24:17–39
- Halle S, Stenseth NC (2000) Activity patterns in small mammals. Springer, Berlin Heidelberg New York
- Le Maho Y, Goffart M, Rochas A, Felbabel H, Chatonnet J (1981) Thermoregulation in the only nocturnal simian: the night monkey *Aotus trivirgatus*. *Am J Physiol* 240:R156–165
- Mann GF (1956) Efecto del frío en mamíferos amazónicos. *Invest Zool Chil* III:155
- Marques MD, Waterhouse JM (1994) Masking and the evolution of circadian rhythmicity. *Chronobiol Int* 11:146–155
- Merritt JF, Vessey SH (2000) Shrews: small insectivores with polyphasic patterns. In: Halle S, Stenseth NC (eds) *Activity patterns in small mammals. An ecological approach*. Springer, Berlin Heidelberg New York, pp 235–252
- Morland HS (1993) Seasonal behavioral variation and its relationship to thermoregulation in ruffed lemurs. In: Kappeler PM, Ganzhorn JU (eds) *Lemur social systems and their ecological basis*. Plenum, New York, pp 193–203
- Morrison P, Simoes J (1962) Body temperatures in two Brazilian primates. *Zoologia* 24:167–178
- Mrosovsky N (1999) Masking: history, definitions, and measurement. *Chronobiol Int* 16:415–429
- Overdorff DJ (1996) Ecological correlates to activity and habitat use of two prosimian primates: *Eulemur rubriventer* and *Eulemur fulvus rufus* in Madagascar. *Am J Primatol* 40:327–342
- Overdorff DJ, Rasmussen MA (1995) Determinants of nighttime activity in “diurnal” lemurid primates. In: Alterman L (eds) *Creatures of the dark: the nocturnal prosimians*. Plenum, New York, pp 61–74
- Perrigo G (1987) Breeding and feeding strategies in deer mice and house mice when females are challenged to work for their food. *Anim Behav* 35:1298–1316
- Perrigo G (1990) Food, sex, time, and effort in a small mammal: energy allocation strategies for survival and reproduction. *Behavior* 114:191–205
- Rappold I, Erkert HG (1994) Re-entrainment, phase-response and range of entrainment of circadian rhythms in owl monkeys (*Aotus lemurinus g.*) of different age. *Biol Rhythm Res* 25:133–152
- Rauth-Widmann B, Thiemann-Jager A, Erkert HG (1991) Significance of nonparametric light effects in entrainment of circadian rhythms in owl monkeys (*Aotus lemurinus griseimembra*) by light-dark cycles. *Chronobiol Int* 8:251–266
- Rietveld WJ, Minors DS, Waterhouse JM (1993) Circadian rhythms and masking: an overview. *Chronobiol Int* 10:306–312
- Rotundo M, Sloan C, Fernandez-Duque E (2000) Cambios Estacionales en el Ritmo de Actividad del Mono Mirikiná (*Aotus azarai*) en Formosa Argentina. In: Cabrera E, Mércolli C, Resquin R (eds) *Manejo de Fauna Silvestre en Amazonía y Latinoamérica*, Asunción, pp 413–417

- Schaik CP van, Kappeler PM (1993) Life history, activity period and lemur social systems. In: Kappeler PM, Ganzhorn JU (eds) Lemur social systems and their ecological basis. Plenum, New York, pp 241–260
- Schaik CP van, Kappeler PM (1996) The social systems of gregarious lemurs: lack of convergence with Anthropoids due to evolutionary disequilibrium? *Ethology* 102:915–941
- Smythe N (1997) The seasonal abundance of night-flying insects in a Neotropical forest. In: Leigh EGJ, Rand SA, Windsor DM (eds) The ecology of a tropical forest. Seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, DC, pp 309–318
- Stallings JR, West L, Hahn W, Gamarra I (1989) Primates and their relation to habitat in the Paraguayan Chaco. In: Redford KH, Eisenberg JF (eds) Advances in neotropical mammalogy. Sandhill Crane, Gainesville, FL, pp 425–442
- Tattersall I (1987) Cathemeral activity in primates: a definition. *Folia Primatol* 49:200–202
- Wallace RB, Painter LE, Taber AB (1998) Primate diversity, habitat preferences, and population density estimates in Noel Kempff Mercado National Park, Santa Cruz Department, Bolivia. *Am J Primatol* 46:197–211
- Warren RD, Crompton RH (1997) A comparative study of the ranging behaviour, activity rhythms and sociality of *Lepilemur edwardsi* (Primates, Lepilemuridae) and *Avahi occidentalis* (Primates, Indriidae) at Ampijoroa, Madagascar. *J Zool Lond* 243:397–415
- Wauters LA (2000) Squirrels—medium-sized granivores in woodland habitats. In: Halle S, Stenseth NC (eds) Activity patterns in small mammals. Springer, Berlin Heidelberg New York, pp 131–144
- Wright PC (1978) Home range, activity patterns, and agonistic encounters of a group of night monkeys (*Aotus trivirgatus*) in Peru. *Folia Primatol* 29:43–55
- Wright PC (1985) The costs and benefits of nocturnality for *Aotus trivirgatus* (the night monkey). City University of New York
- Wright PC (1989) The nocturnal primate niche in the New World. *J Hum Evol* 18:635–658
- Wright PC (1999) Lemur traits and Madagascar ecology: coping with an island environment. *Yearb Phys Anthropol* 42:31–72
- Zielinski WJ (2000) Weasels and martens. Carnivores in northern latitudes. In: Halle S, Stenseth NC (eds) Activity patterns in small mammals. Springer, Berlin Heidelberg New York, pp 95–118