

Cathemerality and Lunar Periodicity of Activity Rhythms in Owl Monkeys of the Argentinian Chaco

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Key Words

Gran Chaco · Seasonality · Activity pattern · Circadian rhythm · *Aotus*

Abstract

Although most South American owl monkeys are mainly nocturnal, *Aotus azarai azarai* of the Argentinian Chaco regularly shows diurnal activity. In this study we examined the strong influence of moonlight on its diurnal and nocturnal activity, as well as the interaction of moonlight effects with other exogenous factors. We analyzed long-term automated activity recordings obtained with accelerometer collars from 7 owl monkeys during 2003 and 2004. Our data show marked lunar periodic and seasonal modulations of the owl monkeys' activity pattern. On full moon days they were active throughout the whole night and displayed reduced activity during the day. With a new moon, activity decreased during the dark portion of the night, peaked during dawn and dusk and extended over the bright morning hours. Waxing and waning moons induced a significant increase in activity during the first and the second half of the night, respectively. During the cold winter months the monkeys displayed twice as much activity throughout the warmer bright part of the day than during the rest of the year. These findings indicate that *A. a. azarai* is mainly a dark-active species, but is still able to shift a considerable portion of activity into the bright part of the day if unfavourable lighting and/or temperature conditions prevail during the night. Copyright © 2006 S. Karger AG, Basel

Introduction

South American owl monkeys (*Aotus* spp.) have long been described as the only simian primates with nocturnal habits [Martin, 1990]. This characteristic was observed in wild individuals in Perú, Bolivia, Paraguay and Argentina [Wright, 1978, 1989; Aquino and Encarnación, 1986; García and Braza, 1989; Arditi, 1992], as well

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as in individuals kept in outdoor enclosures in Panamá [Moynihan, 1964]. The unquestionable nocturnal habits of owl monkeys notwithstanding, it has also become evident that the extent of their activity during the night is strongly dependent on the amount of moonlight.

The strong effects of moonlight on the nocturnal activity of owl monkeys were first investigated on the North Colombian *A. lemurinus griseimembra* [Erkert, 1974, 1976]. Automated activity recordings carried out under semi-natural conditions were convincingly corroborated by field observations of the nocturnal habits of the species. Owl monkeys showed a luminance-dependent activity optimum at approximately 0.1–0.5 lux, a light intensity that corresponds to the brightness of the night sky at full moon. A second study revealed that the changes in nocturnal activity that take place with different amounts of moonlight could be induced in the laboratory by simulating the nightly luminance pattern at the four phases of the moon (new, waxing, full and waning) with corresponding rectangular light-dark cycles [Erkert and Gröber, 1986]. Thus, both observational and experimental evidence suggested that the luminance prevailing during the night hours is a strong determinant for the expression of nocturnal motor activity in owl monkeys.

More recently, a study of *A. a. azarai* in the North Argentinean Chaco [Fernandez-Duque, 2003; Rotundo et al., 2000] confirmed previous reports that this is the only owl monkey species known to show a considerable amount of diurnal activity [Wright, 1989; Arditi, 1992; Fernandez-Duque and Bravo, 1997]. The animals displayed as much activity during the light phase as they did during the dark phase of the 24-hour cycle; and the amount of moonlight influenced nocturnal activity as well as diurnal activity. Following these results, it seems reasonable to question whether the owl monkeys of the South American Chaco should be considered a true nocturnal species or a cathemeral one.

The term ‘cathemeral’ was introduced by Tattersall [1987] to describe an unusual activity pattern found in several Madagascan lemur species where animals may be active both during day and night [Engqvist and Richard, 1991; Overdorff and Rasmussen, 1995; Colquhoun, 1998; Curtis et al., 1999; Donati et al., 2001; Curtis and Rasmussen, 2002; Kappeler and Erkert, 2003]. The term cathemerality turned out to be of great heuristic value because it stimulated several field studies in Madagascar that examined some of the proximate factors underlying the expression of diurnal and nocturnal behaviour in various cathemeral lemur species. Furthermore, the discussions generated by studies of the probable ultimate factors leading to the evolution of this unusual activity pattern among primates revived the still open question of how diurnal behaviour may have evolved in an originally nocturnal species [van Schaik and Kappeler, 1996; Kappeler and Erkert, 2003].

Any attempt to examine the origins of diurnality in primates will undoubtedly benefit from a thorough investigation of the causative and modulating environmental factors influencing the cathemeral activity of the Argentinean owl monkeys. The successful adaptation of this species to the harsher conditions of the Gran Chaco, at the southern end of the distribution of the genus, may have been possible only through the evolution of specific behavioural adaptations enabling individuals to exploit habitat resources during the night, as well as during the day. Thus, together with the Madagascan *Eulemur* species, the South American *Aotus* monkeys represent a suitable model to study how the transition from a primarily nocturnal lifestyle to a more diurnal one may have proceeded in primates.

The formulation and testing of hypotheses about the evolution of activity patterns in primates require reliable and continuous activity data collected during months or years. To that end, we carried out automated long-term activity recordings in several individuals of *A. a. azarai* using accelerometer/data logger devices that allow uninterrupted recordings over a span of 6 months. These devices had already been used for long-term activity recordings in red fronted lemurs (*Eulemur fulvus rufus*) and Verreaux's sifakas (*Propithecus verreauxi verreauxi*) in Western Madagascar [Kappeler and Erkert, 2003; Erkert and Kappeler, 2004].

Methods

Study Site and Subjects

The study area, which includes a mosaic of grasslands, savannas, dry and gallery forests, is located in a subtropical area of South America (58°11' W, 25°58' S) at approximately 60 m above sea level. The region is characterized by a pronounced seasonality of rainfall, temperature, day length and food availability [Fernandez-Duque et al., 2002].

In the Argentinean provinces of Formosa and Chaco, the gallery forests of the Río Paraguay and its tributaries are the habitat of the owl monkey subspecies *A. a. azarai* [Brown and Zunino, 1994]. The owl monkey population found on the borders of Riacho Pilagá in the Province of Formosa has been monitored regularly since 1997 [Fernandez-Duque and Bravo, 1997; Fernandez-Duque et al., 2001; Fernandez-Duque, 2005]. Five of the social groups in that population were the focus of a 1-year observational study of activity patterns conducted between 1998 and 1999 [Rotundo et al., 2000; Fernandez-Duque, 2003]. One hundred and fifteen animals in the study population have been marked and/or radio collared to allow reliable identification of individuals in this sexually monomorphic species [Fernandez-Duque and Rotundo, 2003].

In order to carry out uninterrupted long-term activity recordings over 6-month periods, owl monkeys were fitted with accelerometer collars that automatically record activity and store the data until downloaded to a computer (see section below). For the first recording period, the Actiwatch AW4 devices were inserted into a small waterproof aluminum box attached to a plastic-coated stainless steel strip [Erkert and Kappeler, 2004]. For the second recording period, the devices were protected only by several layers of broad adhesive tape (Tesaband) coated by a thin acrylic spray layer. Four male and 4 female owl monkeys from eight different social groups were fitted with these collars in March 2003. Between September and November 2003, three additional accelerometer collars were fitted on 2 males and 1 female. All subjects were reproducing adults mated to radio-collared individuals to facilitate locating the animals fitted with the accelerometer collars. Unfortunately, 2 males and 1 female disappeared from their groups after being replaced by incoming same-sex adults [Fernandez-Duque, 2004]. Therefore, their collars and the stored activity data were lost. In addition, one of the devices failed, making 7 the total number of individuals contributing data.

Owl monkeys were captured by anaesthetising them with small doses of ketamine hydrochloride (50 mg/kg; Vetanarcol, König, Argentina) loaded in disposable darts administered with a blowpipe or rifle [Fernandez-Duque and Rotundo, 2003]. Before fixing the Actiwatch collar, the individuals underwent a detailed physical examination including the taking of various morphological measurements and the collection of biological samples for genetic analyses. Following these procedures, and after the sedation effects had worn off, the animals were released close to their social group. They were subsequently observed until they rejoined their group. All collared individuals had been monitored regularly throughout the preceding years and were also monitored several times a month during the period of activity recordings presented here. This allowed changes in group composition that could have affected the social status of the subject and potentially its pattern of activity to be recorded. Repeated observations of the individual during the days following darting indicated that the capture and subsequent treatment had neither direct adverse effects on the animals' behaviour nor on their social status within the group. Data on the subjects and recording periods are summarized in table 1.

Table 1. Sex, estimated age, group size and length of recording period for all *Aotus* subjects

Name	Sex	Estimated age years	Group size	Recording period months
Victor	m	>4	3	5.7
Eulogia	f	>5	3	5.0
Irene	f	>5	4	5.6
Fumata	f	>5	3	5.2
Pampero	m	>5	5	3.1
Fabian	m	>4	2	5.2
Anacleto	m	>5	5	6.1

Rainfall, Temperature and Light Data

Rainfall and temperature data are summarized in figure 1. The monthly amounts of rainfall were obtained from records kept at Estancia Guaycolec since 1977. Ambient temperature was measured hourly with a Stowaway XTI data logger, set up in the camp at the entrance to the study area. Luminance (lux) was measured at 5-min intervals using an Actiwatch-L plus[®] actimeter/luxmeter data logger device with remote photocell from Cambridge Neurotechnology, UK. This device can automatically record light measurements in the 0.01–65,000 lux range and store the data collected for approximately 30 days. It was placed in a small watertight transparent acrylic box fixed on top of a 2-metre-high post situated about 50 m from the edge of the forest, with the photocell directed upwards to the zenith. Light data were downloaded monthly to a computer using an SF Actiwatch Reader interface and the Actiwatch-Sleep 2001 software (Cambridge Neurotechnology). The dates of the four phases of the moon, local times of sunset (SS), sunrise (SR) and end and onset of the astronomical twilight (EAT, OAT) were obtained from the U.S. Naval observatory website (<http://aa.usno.navy.mil/data>).

Data Analysis and Statistics

After 5–6 months of activity recording the monkeys were recaptured and the collars removed. The activity data stored on the AW4 devices were downloaded using the ‘actiwatch/sleepwatch’ program (Cambridge Neurotechnology). The data files were then reformatted and processed with an improved program for periodogram analysis and double plot creation [Dörrscheidt and Beck, 1975]. Further data analyses were done with commercially available software from Cambridge Neurotechnology (sleepwatch program), SPSS (statistics) and SigmaPlot (graphics).

In order to characterize the owl monkeys’ pronounced bimodal activity pattern (fig. 2b) and to analyze its modulation by moonlight and/or exogenous factors, we used the following parameters: the average amount of activity per day, the average duration of the activity time per day (alpha) and the evening onset and morning end of the activity time (OA, EA), as well as the time, height and duration of the evening and morning activity peaks (EPT, MPT; EPH, MPH; EPD, MPD) and the peak-to-peak intervals (PPIs).

Because of the marked lunar periodic modulation of the owl monkeys’ activity pattern [Fernandez-Duque, 2003], the evaluation of the activity data had to be done in two ways, first considering the quite different time course of motor activity during the four phases of the moon and second by disregarding this prominent periodicity.

For doing the analyses considering the moonlight effects on the monkeys’ diel activity pattern through the year, daily activity for each individual from the day before, during and after each moon phase was averaged in 1-hour bins. These 1-hour means, obtained as a percentage of the respective average total activity per day, were then used to calculate the percentage activity within 3-hour periods for a typical 24-hour period at each moon phase. Resulting data were then av-

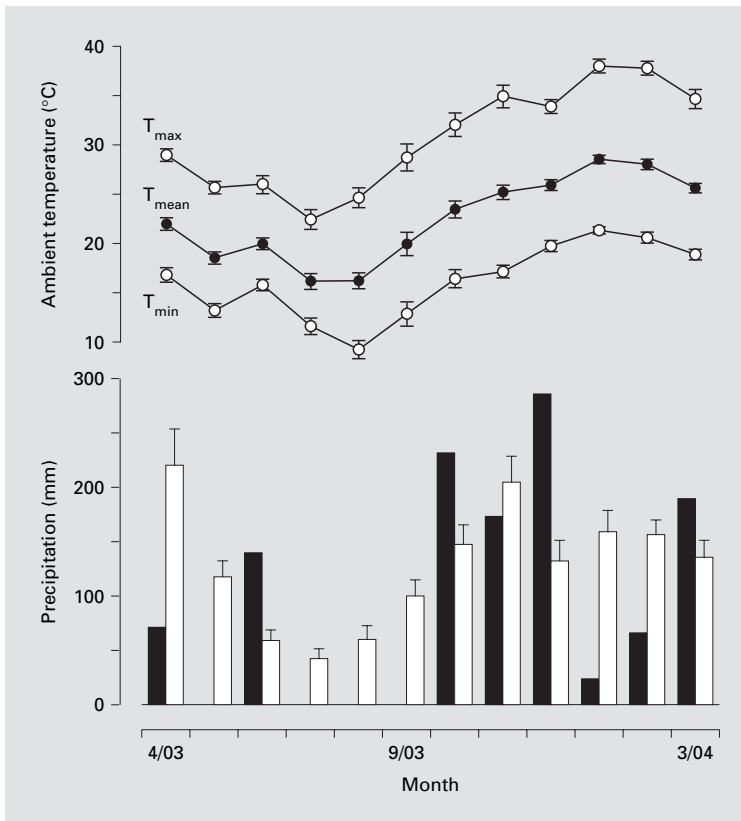


Fig. 1. Annual variation of monthly (30 days) averages of daily minimum, mean and maximum temperature (lines) and monthly precipitation (solid black bars) during the recording period from April 2003 to March 2004 and long-term monthly precipitation average (27 years, solid white bars) at Estancia Guaycolec, Formosa, Argentina.

eraged over the short and long day months or over the whole year. To evaluate the influence of various environmental factors through the year, for each individual we averaged the time series of the recorded 5-min activity data of each of the successive lunar cycles over 24 h, starting from the new moon phase on April 1, 2003. From the resulting diel mean activity patterns per lunar month, calculated as a percentage of the overall mean of 24-hour total activity (fig. 2b), we then determined the various parameters characterizing the pronounced bimodal activity pattern [see above and Erkert and Kappeler, 2004].

The resulting individual activity data for the successive lunar cycles were then correlated with various environmental data obtained on total rainfall and average temperatures over the respective time periods. To correlate activity parameters with astronomical ones, i.e. times of SS and SR, EAT, OAT, and night length (NL), we obtained the data for the midmonth day of the respective month from the relevant tables.

For statistical analyses we conducted non-parametric Spearman correlation analyses, as well as non-parametric Friedman and Wilcoxon tests according to Weber [1972]. Probabilities of error smaller than 0.05 were considered statistically significant.

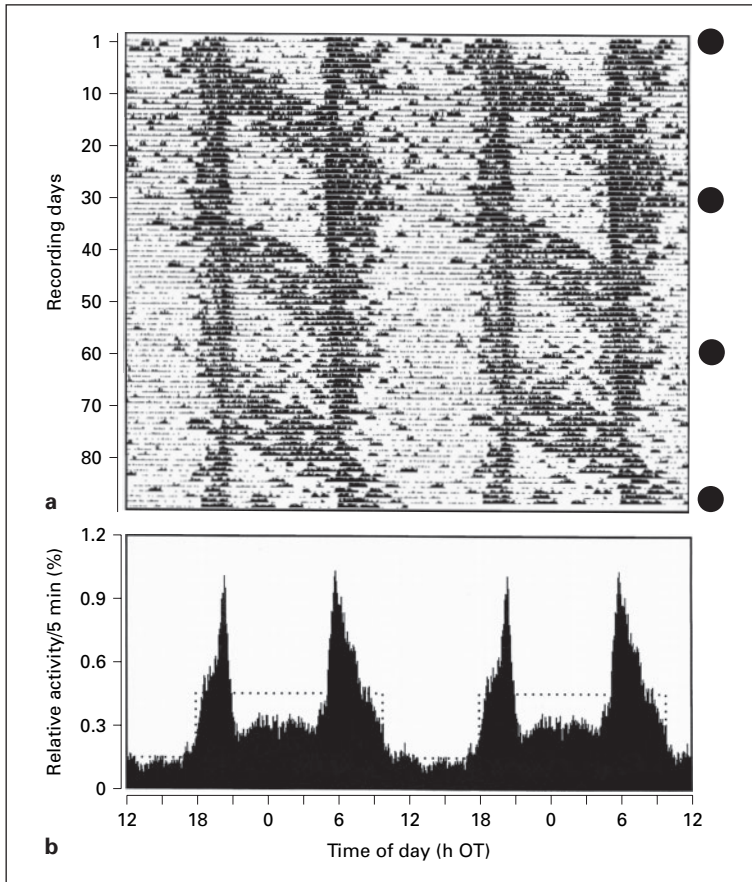


Fig. 2. a Double plot of original activity recordings in a male *A. a. azarai* over a period of 3 months from November 2003 to February 2004 (top to bottom). Line spaces between the histograms correspond to 100 counts per 5-min bin. Note the pronounced lunar periodic course of nighttime activity and that around new moon (solid black circles on right margin of panel) only a little motor activity is produced throughout the night, while much more activity occurs throughout the morning hours than at the other phases of the moon. **b** Double-plotted bimodal activity pattern of this owl monkey as averaged over the whole recording period shown above. During the nighttime from 21.00 to 6.00 h, the average level of activity is considerably higher than during bright hours of the day. The dotted square wave pattern indicates the calculated average activity time (α) and resting time (ρ).

Results

Effects of Lunar Periodic Variation on Activity

The diel pattern of motor activity in the North Argentinean owl monkeys underwent very pronounced lunar periodic variations as shown by a double plot of the activity recording in a male *Aotus* over a period of 3 months from November 2003 to February 2004 (fig. 2). The most regular part of diel activity occurred during

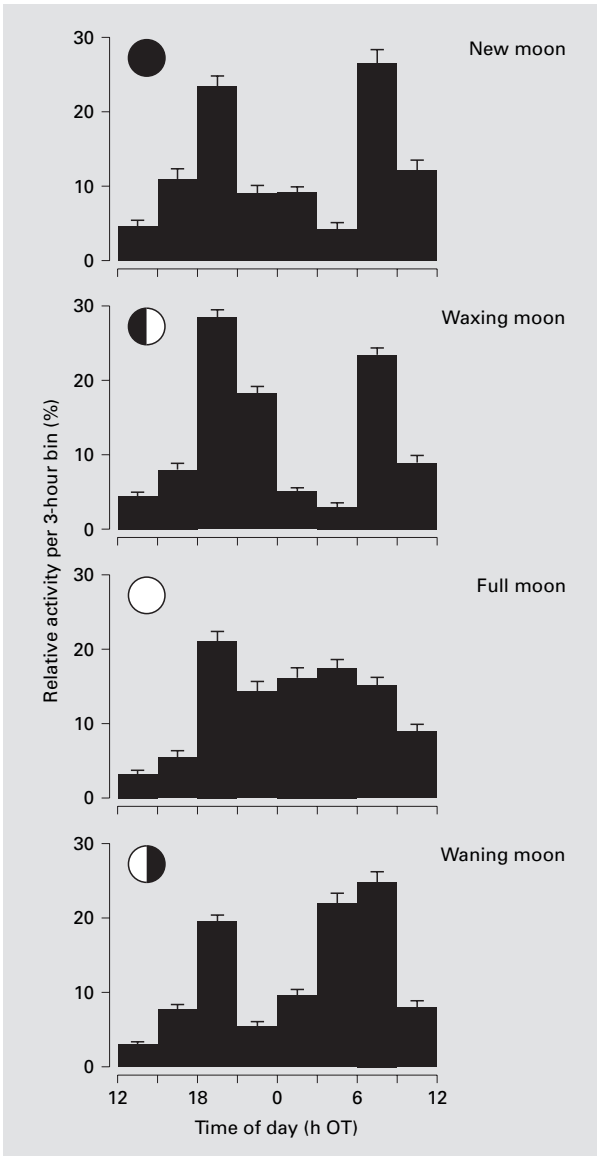


Fig. 3. Lunar periodic variation of the activity pattern in wild *A. a. azarai* (5 individuals, 23 lunar cycles during five short day months from April to September) as indicated by the relative amount of activity (mean \pm SE) developed in successive 3-hour periods at the four phases of the moon.

the periods of astronomical twilight with two main peaks of activity from 18.00 to 21.00 h and from 5.00 to 8.00 h. Between those two peaks, significant amounts of activity occurred regularly during only the moonlit parts of the night. During the dark parts of the night, only very few and shorter bouts of activity were observed.

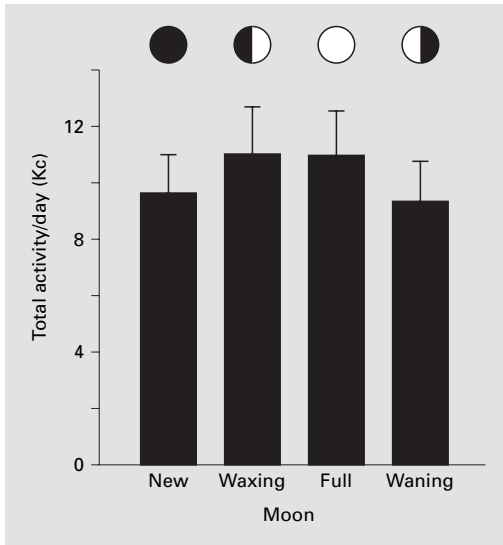


Fig. 4. Average amount of total activity per day in thousand counts per day + SE at new, waxing, full and waning moon (7 individuals, 33 lunar cycles).

Table 2. Comparison of average total activity per day at the four phases of the moon

Compared data	u	p
new < waxing moon	2.67	< 0.01
new < full moon	2.76	< 0.01
new > waning moon	2.24	< 0.05
waxing > full moon	0.87	>> 0.05
waxing > waning moon	3.23	< 0.001
full > waning moon	3.76	< 0.001

Results of Wilcoxon tests for significant differences between moon phases (7 individuals, 33 lunar cycles).

Around the period of new moon, the dark period corresponded to the whole astronomical night, in other words to the time between the end and onset of astronomical twilight. During waxing and waning moons, the monkeys strongly reduced their activity during the second and first half of the night, respectively.

Averaging the individuals' data over several months clearly showed *A. a. azarai* to be a more nocturnal than diurnal species (fig. 2). However, the monkeys also displayed a considerable amount of motor activity throughout the solar day. This occurred mainly during the morning from SR to noon, and predominantly during the days around new moon and waning moon (fig. 2 and 3).

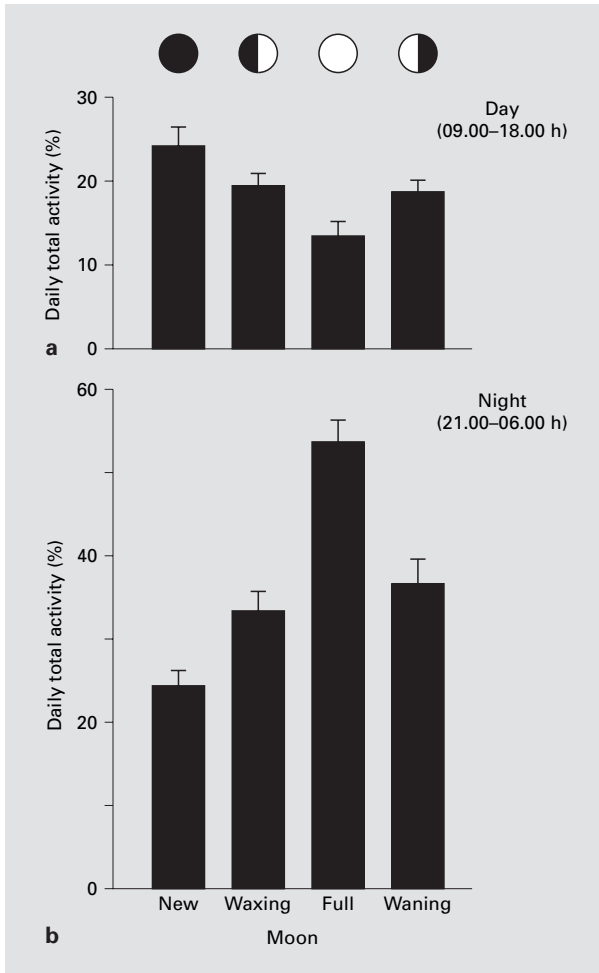


Fig. 5. Lunar effects on the relative amount of motor activity (percentage of 24-hour total; mean + SE) produced during the bright hours of the day from 9.00 to 18.00 h (a) and during the night from 21.00 to 6.00 h (b).

An activity pattern that changes periodically in parallel to the moonlit part of the night is indeed characteristic for the species, as shown by the relative amount of activity during 3-hour intervals (fig. 3). The full moon activity pattern was clustered and tended to have a unimodal time course, whereas the patterns became clearly bimodal for the other phases of the moon. Main activity was concentrated in the first half of the night at waxing moon, and during the second half of it at waning moon. The total amount of motor activity also varied significantly with the lunar phase (fig. 4; Friedman test: $\chi^2 = 27.69$; $p < 0.001$). Activity during waxing or full moon was significantly higher than activity during waning or new moon as indicated by Wilcoxon tests (table 2).

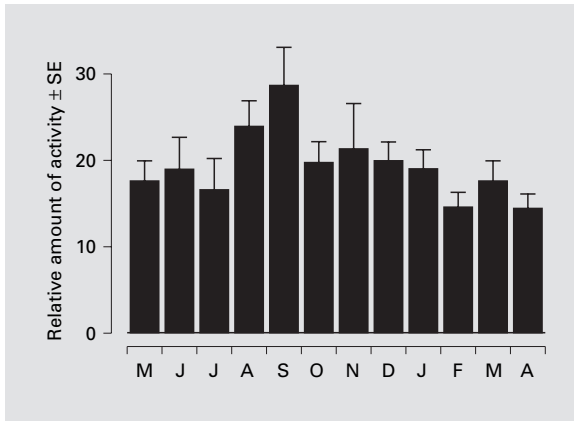


Fig. 6. Seasonal variation in the relative amount of activity produced during the bright hours of the day from 9.00 to 18.00 h. Mean values + SE as averaged over the data for the four phases of the moon (cf. fig. 5a; 5 individuals for the short-day lunar months from April/May to September/October, and 2 individuals for the long-day lunar months from September/October to March/April of the year).

Lunar effects on motor activity become especially striking when comparing the relative amount of total daily activity that occurred during the dark nighttime from 21.00 to 6.00 h at the four phases of the moon (fig. 3, 5). More than half ($53 \pm 3\%$) of daily total activity took place during the night around full moon, whereas only a fourth ($24 \pm 2\%$) of daily total activity took place during the night at new moon. Approximately one third of total daily activity occurred during waxing moon ($33 \pm 2\%$) and waning moon ($36 \pm 3\%$). This high variation of night activity with changing moon phases was statistically significant as indicated by Friedman test ($\chi^2 = 26.7$; $p < 0.001$). Wilcoxon tests revealed significant differences among the data for all compared moon phases ($p < 0.01$ with only one exception of $p < 0.05$).

During the bright hours of the day (9.00 to 18.00 h), the largest portion of the total daily activity occurred at new moon while the least amount of activity took place around full moon (fig. 5; Friedman test: $\chi^2 = 39.9$, $p < 0.001$). Wilcoxon tests carried out using the monthly averages of relative activity showed significant differences ($p < 0.05$) between new and waxing or waning moon, as well as between waxing and full moon, and highly significant differences ($p \leq 0.01$) between full and new or waning moon. Only the difference between waxing and waning moon data did not reach statistical significance.

Effects of Astronomical and Environmental Factors on Activity

The relative proportion of daytime and nighttime activity on the owl monkeys' 24-hour total varied significantly with the moon phase, and also over the year (9.00–18.00: fig. 6; Friedman test: $\chi^2 = 21.65$, $p < 0.05$; 21.00–6.00: $\chi^2 = 20.1$, $p < 0.05$). Highest levels of daytime activity were observed during August–September, when night activity was concurrently lowest. On the other hand, daytime activity reached its minimum during January–February, when night activity was highest.

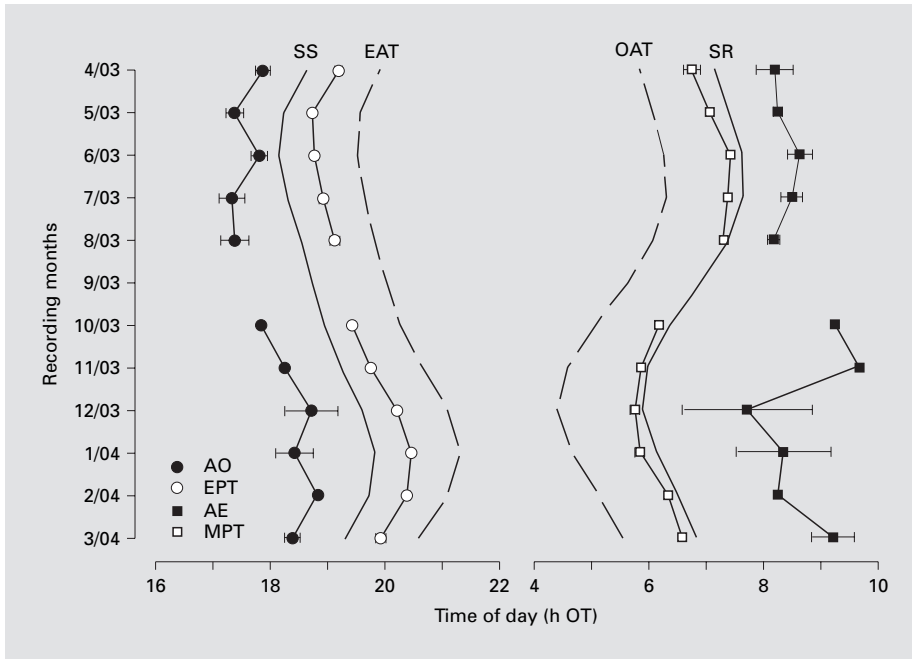


Fig. 7. Annual variation of onset and end of activity (AO, AE) and of EPT and MPT of the average monthly activity pattern (arithmetic means \pm SE) in wild *A. a. azarai* in relation to the corresponding mean times of SS and SR, and the corresponding mean times of EAT and OAT. Ordinate values from top to bottom represent the data for successive calendar months (5 individuals for the short-day months from April to August 2003 and 2 individuals for the long-day months from October 2003 to March 2004).

The annual changes in various parameters of the owl monkeys' activity pattern co-varied at least partially with the annual changes in astronomical parameters. The times of evening OA and morning EA, as well as the EPT and MPT changed across months, and this annual variation occurred more or less in parallel to the annually changing times of SS and EAT or to the times of SR and OAT, respectively. The timing of the two activity peaks, however, showed a much closer relationship to these astronomical parameters than the onset and end of activity (fig. 7).

In other words, the timing of the two activity peaks showed a much higher correlation with the respective astronomical parameters than the times of onset and end of activity (SS vs. EPT, $r = 0.933$; SS vs. OA, $r = 0.600$; SR vs. MPT, $r = 0.89$; SR vs. EA, $r = -0.02$).

On the other hand, the annual changes in some other activity parameters were not very strongly correlated to the variation in environmental factors. For example, the monthly average of daily total activity did co-vary, only slightly, with precipitation ($r = 0.390$, $p = 0.025$) and ambient temperature (TA mean: $r = 0.360$, $p = 0.04$; TA min.: $r = 0.384$, $p = 0.027$; TA max.: $r = 0.357$, $p = 0.042$) but not with NL ($r = -0.241$, $p = 0.18$), sunset ($r = 0.142$, $p = 0.432$), or sunrise ($r = -0.302$, $p = 0.088$).

As expected, the animals started activity later with later sunset ($r = 0.600$, $p < 0.001$) and later end of astronomical twilight ($r = 0.598$, $p < 0.000$), as well as on warm (TA max.: $r = 0.754$, $p < 0.001$) and rainy days ($r = 0.620$, $p < 0.000$). The end of activity did not correlate significantly with sunrise ($r = -0.02$, $p = 0.904$) or ambient temperature (TA max.: $r = 0.15$, $p = 0.388$), but it showed an almost significant positive correlation with precipitation ($r = 0.343$, $p = 0.051$) which indicates a certain tendency to terminate activity later on rainy days. The activity time alpha did not correlate significantly with the times of SS ($r = -0.292$, $p = 0.099$), SR ($r = 0.323$, $p = 0.67$), or even NL ($r = 0.299$, $p = 0.090$), but showed a negative correlation with ambient temperature (TA max.: $r = -0.356$; $p = 0.042$) indicating that the animals shortened their activity time on warmer days.

The parameters characterizing the pronounced bimodal activity pattern of *Aotus* showed different correlations with the annually changing astronomical parameters and climatic factors. As expected, EPT, MPT, the PPI, EPH and MPD were significantly positively or negatively correlated with the times of sunset, sunrise, evening end and morning onset of astronomical twilight, as well as with ambient temperature ($p \leq 0.002$ each). On the other hand, the EPD did not correlate with any of these parameters, nor was the MPH correlated with ambient temperature. The parameters EPT ($r = 0.361$, $p = 0.039$), MPT ($r = -0.44$, $p = 0.01$), and the PPI ($r = -0.371$, $p = 0.033$) showed slight co-variation with precipitation, while the EPH and MPD were significantly negatively or positively correlated with it ($r = -0.465$, $p = 0.006$ and $r = 0.505$, $p = 0.003$, respectively).

Cross-correlation analyses testing the relationship between the various parameters of the owl monkeys' bimodal monthly mean activity pattern mostly yielded the expected positive or negative correlations. Surprisingly, however, the monthly average of daily total activity was negatively correlated with the EPH and MPH (EPH: $r = -0.546$, $p = 0.001$; MPH: $r = -0.540$; $p = 0.001$), but not with the EPD ($r = 0.104$, $p = 0.566$) and only slightly with MPD ($r = 0.396$, $p = 0.022$).

Discussion

Our quantitative long-term activity recordings clearly indicate that *A. a. azarai* is a predominantly nocturnal species in the Argentinean Chaco. During the night hours (21.00–6.00 h), they showed, on average, twice as much motor activity than during the day (9.00–18.00 h). However, the monkeys usually started their nocturnal activity well before SS and terminated it considerably after SR. This pattern resulted in two pronounced activity peaks, each comprising, on average, about 22% of daily total activity that occurred during the twilight periods within the time windows from 18.00 to 21.00 h and 6.00 to 9.00 h.

Although more daytime activity has been reported in previous studies of this species [Arditi, 1992; Rotundo et al., 2000; Fernandez-Duque, 2003], this difference is mainly due to differing definitions of day- and nighttime. For instance, Fernandez-Duque [2003] referred owl monkey activity data to the nautical night and day or the spans between the end and onset of nautical twilight (centre of sun 12° below horizon). In the present study we examined the monkeys' mostly pronounced bimodal activity pattern with high peaks during the twilight times and compared the activity data of four fixed time spans comprising the central night and day hours

(21.00–6.00 h and 9.00–18.00 h), as well as the two twilight periods (18.00–21.00 and 6.00–9.00 h).

Furthermore, it is also possible that some of the differences between estimates of the night- and daytime activity may be due, to a certain extent, to the difficulties of obtaining accurate estimates of the owl monkeys' behavioural activities during the darker night hours. Determining the activity of *Aotus* by listening for vocalizations, movements and the dropping of food items [Wright, 1989; Fernandez-Duque, 2003], even with the help of night vision goggles, will obviously tend to underestimate the frequency and nature of activity at night. In contrast, our method of recording activity based on positive or negative accelerations of the data logger device attached to a collar, not only records displacements from climbing and jumping, but also captures less conspicuous movements the animals regularly make while foraging within a particular tree or interacting socially. Our results convincingly show that carrying out automated long-term activity recordings using an accelerometer/data logger device, is one of the best ways to collect reliable quantitative data on motor activity in wild nocturnal primates or other medium-sized mammals.

Consistent with previous reports, this study shows that the activity pattern of owl monkeys is profoundly influenced by moon phase. Lunar periodic changes of activity have been observed in several South American *Aotus* species. Marked activity-enhancing effects of moonlight were first described in captive *A. l. griseimembra* recorded in Colombia under natural lighting conditions [Erkert, 1974, 1976]. Field observations in Peruvian and Bolivian owl monkeys then indicated increased nocturnal motor and vocalization activity on full moon nights [Wright, 1978, 1989; Aquino and Encarnación, 1986; García and Braza, 1987, 1993]. Strong moonlight effects were also recently found in *A. a. azarai* of the Argentinean Chaco [Fernandez-Duque, 2003]. Our uninterrupted long-term recordings revealed an even stronger lunar periodic variation of the owl monkeys' nocturnal activity pattern than that found by observational studies. Similarly pronounced lunar periodic variations of the activity pattern have been reported only from the activity recordings carried out on captive Colombian owl monkeys [Erkert, 1974]. This indicates that quantitative activity recordings in captive monkeys, held under semi-natural conditions within the distribution area, may provide reliable data for a sufficiently good estimation of activity in wild individuals. Hence, adequate quantitative activity records in individuals kept in large outdoor enclosures under semi-controlled conditions may offer a useful tool for analysing the effects of certain environmental factors, such as food availability, precipitation and luminance, on the owl monkeys' diel, lunar and annual activity rhythm.

The immediate reaction to sudden variations of dim light intensities found in *A. l. griseimembra* [Erkert, 1974; Erkert and Gröber, 1986] suggest that also the inhibiting, disinhibiting or enhancing effects of luminosity on the motor activity of *A. azarai* most probably represent rhythm masking direct effects. This very strong dependency of motor activity on dark time luminosity has been demonstrated by laboratory experiments in *A. l. griseimembra*. These monkeys engaged in maximal activity when exposed to artificial 12:12 h light-dark cycles with 0.1–0.5 lux in the dark time, which approximately corresponds to the brightness of full moon nights, while lower and higher luminosities in the dark time led to considerably reduced activity [Erkert, 1976]. By varying the light intensity during the dark time, the monkeys' activity pattern could be changed in a predictable manner [Erkert and Gröber, 1986].

However, the monkeys continued to synchronize their endogenous (circadian) activity phase to the dark time when the optimal luminosity of 0.1–0.5 lux was given during the light time of a 12:12 h light-dark cycle, and suboptimal (i.e. strongly activity inhibiting) low light intensities were given during the dark time. This ‘dark switch’ of the circadian rhythm indicated that *Aotus* is a genuine dark active genus [Erkert and Thiemann-Jäger, 1983].

Despite a predominantly nocturnal activity rhythm, *A. a. azarai* also showed a considerable amount of activity during the bright portion of the 24-hour day. Their motor activity was not evenly distributed over the 24-hour cycle, but showed a distinct bimodal time course with pronounced peaks during astronomical dawn and dusk. Thus, the proportion of diurnal activity is considerably increased if one adds the amount of activity displayed during the 1–2 h before SS and after SR when luminosity may reach or exceed 500–1,000 lux. As observed in previous studies [Fernandez-Duque, 2003], daytime activity levels were highest and lowest following new and full moon nights, respectively (fig. 5). This result may indicate that the monkeys’ daytime activity represents, at least partly, a compensatory reaction to the low-light-induced inhibition of activity throughout their preferred activity period at night.

The amount of diurnal activity increased throughout the austral winter. Diurnal activity was most pronounced during months when ambient temperature tended to be lowest. This finding is also supported by the negative correlation found between the average activity time and ambient temperature. When temperatures are low, it is common to observe the monkeys huddling during the coldest hours of dawn and climbing to the top of tree crowns to sunbath as soon as the sun rises. Conversely, when days are very warm, all of the diurnal activity is concentrated during the early hours in the morning and the late hours in the evening. An apparent behavioural adjustment to cold days has also been reported in *A. a. boliviensis* and *Galago moholi* [Bearder et al., 2006]. For example, although *A. a. boliviensis* is nocturnal in Bolivia [García and Braza, 1987, 1993], some anecdotal evidence suggests that during unusually cold weather (6–7 °C) owl monkeys foraged during the day [Mann, 1956].

It is becoming clear that in order to develop a comparative framework for the analysis of the growing literature on cathemeral primates it will be necessary to define unambiguously certain regularly used terms. For example, when assessing the activity pattern of *A. azarai*, Fernandez-Duque [2003] used the times of the end and beginning of nautical twilight as reference phases. That led to a considerably higher degree of ‘light activity’ than would have resulted if the times of SS and SR had been used instead.

Cathemerality was initially defined as follows: ‘the activity of an organism may be regarded as cathemeral when it is distributed evenly throughout the 24 h of the daily cycle, or when significant amounts of activity occur within both the light and dark portions of that cycle’ and ‘cathemeral primates are as active at various periods during the night, as during the hours of daylight’ [Tattersall, 1987]. However, terms like ‘daylight’ or ‘dark and light portion’ need to be defined in a quantitative and measurable way. This can be accomplished by giving a certain threshold of luminosity, astronomically relating them to certain phases of the solar cycle such as SS and SR, or to the times of the end and beginning of civil, nautical or astronomical twilight. In chronobiology, the times of SS and SR have usually been chosen as refer-

ence phases of the natural light-dark cycle [Erkert, 1974, 1976; Daan and Aschoff, 1975; Erkert and Kappeler, 2004]. To avoid confusion and obtain comparable data in the future, we propose the use of the more 'classic' reference times of SS and SR.

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