

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

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Abstract

Although most South American owl monkeys are mainly nocturnal, *Aotus azarai azarai* of the Argentinean Chaco regularly shows diurnal activity. In this study we examined the strong

influence of moonlight on their 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 seven 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 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 moon induced a significant increase in activity during the first and 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, 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.

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 living individuals in Perú, Bolivia, Paraguay and Argentina (Aquino and Encarnación 1986; Arditi 1992; García and Braza 1989; Wright 1978; Wright 1989), as well 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; Erkert 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 moon) with corresponding rectangular light-dark cycles (Erkert and Groeber 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, an intensive observational 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 (Arditi 1992; Fernandez-Duque and Bravo 1997; Wright 1989). The animals displayed as much

activity during the light-phase as they did during the dark-phase of the 24-hr cycle; and the amount of moonlight influenced the nocturnal activity, as well as the diurnal one. 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 (Colquhoun 1998; Curtis and Rasmussen 2002; Curtis et al. 1999; Donati et al. 2001; Engqvist and Richard 1991; Kappeler and Erkert 2003; Overdorff and Rasmussen 1995). The term cathemerality turned out to be of large 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 (Kappeler and Erkert 2003; van Schaik and Kappeler 1996).

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 genus distribution, may only have been possible 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 six 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*) in Western Madagascar (Erkert and Kappeler 2004; Kappeler and Erkert 2003).

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 2005; Fernandez-Duque and Bravo 1997; Fernandez-Duque et al. 2001). Five of the social groups in that population were the focus of a one-year observational study of activity patterns conducted between 1998-1999 (Fernandez-Duque 2003; Rotundo et al. 2000). 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 six 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 in a small water proof aluminum box attached to a plastic coated stainless steel strip (see Erkert and Kappeler 2004). For the second recording period the devices were only protected by several layers of broad adhesive tape (Tesaband) coated by a thin acrylic spray layer. Four male and four 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 two males and one female. All subjects were reproducing adults mated to radio-collared individuals to facilitate locating the animals fitted with the accelerometer collars. Unfortunately, two males and one 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. Finally, one of the devices failed, making seven the total number of individuals contributing data.

Owl monkeys were captured by anaesthetising them with small doses of Ketamine hydrochloride (50 mg/kg; Vetanarcol, Konig, 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 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 us to record changes in group composition that could have affected the social status of the subject and potentially its pattern of activity. Repeated observations of the individual during the following days 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.

INSERT TABLE 1 HERE

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 (United Kingdom). This device can automatically record light measurements in the 0.01- 65000 Lux range and store the data collected for approximately 30 days. It was placed in a small water tight transparent acrylic box fixed on top of a two-meter 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, UK). The dates of the four phases of the moon, local times of sunset, sunrise, and end and

onset of the astronomical twilight were obtained from the U.S. Naval observatory website (<http://aa.usno.navy.mil/data>).

INSERT FIGURE 1 HERE

Data analysis and statistics

After five to six 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, UK). The data files were then reformatted and processed with an improved program for periodogram analysis and double plot creation (Doerrscheidt 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 (c.f. Figure 2, below) and to analyze its modulation by moonlight and/or exogenous factors we used the following parameters: the average amount of activity per day (AA24), 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 timing, height, and duration of the evening and morning activity peaks (EPT, MPT; EPH, MPH; EPD, MPD), and the peak-to-peak intervals (PPI).

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 1h bins. These 1h means, obtained as a percentage of the respective average total activity per day, were then used to calculate the percentage activity within 3h periods for a typical 24-h period at each moon phase. Resulting data were then averaged 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 hrs, 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-h total activity, (c.f. Figure 2, diagram below) 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 (times of sunset and sunrise (SS, SR), end and onset of astronomical twilight (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.

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 three months from November 2003 to February 2004 (Figure 2). The most regular part of diel activity occurred during the periods of astronomical twilight with two main peaks of activity from 1800 to 2100 h and from 0500 to 0800 h. Between those two peaks, significant amounts of activity occurred regularly only during the moonlit parts of the night. During the dark parts of the night, only very few and shorter bouts of activity were observed. 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 moon, 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 (Figure 2). However, the monkeys also displayed a considerable amount of motor activity throughout the solar day. This occurred mainly during the morning from sunrise to noon, and predominantly during the days around new moon and waning moon (Figures 2 and 3).

INSERT FIGURE 2 HERE

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 3h intervals (Figure 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.

INSERT FIGURE 3 HERE

The total amount of motor activity also varied significantly with the lunar phase (Figure 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).

INSERT FIGURE 4 HERE

INSERT TABLE 2 HERE

Lunar effects on motor activity become especially striking when comparing the relative amount of total daily activity that occurred during the dark night time from 2100 to 0600 at the four phases of the moon (Figures 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 $p < 0.05$).

INSERT FIGURE 5 HERE

During the bright hours of the day (0900 to 1800h), the largest portion of the total daily activity occurred at new moon while the least amount of activity took place around full moon (Figure 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 ($p = 0.01$) 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 night time activity on the owl monkeys' 24-h total varied significantly with the moon phase, and also over the year (09:00-18:00: Fig. 6; Friedman test: $\chi^2 = 21.65$, $p < 0.05$; 21:00-06:00: $\chi^2 = 20.1$, $p < 0.05$). Highest levels of daytime activity occurred during August-September, when night activity was concurrently lowest. On the other hand, daytime activity reached its minimum during January-February, when night activity reached highest values.

INSERT FIGURE 6 HERE

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 onset (OA) and morning end (EA) of activity, as well as the timing of the evening and morning peak times (EPT and MPT) changed across months, and this annual variation occurred more or less in parallel to the annually changing times of sunset and end of astronomical twilight (SS and EAT) or to the times of sunrise and onset of astronomical twilight (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 (Figure 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, $r = -0.02$)

INSERT FIGURE 7 HERE

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: $r = 0.384$, $p = 0.027$; TAmix: $r = 0.357$, $p = 0.042$) but not with night length ($r = -0.241$, $p = 0.18$), sun set ($r = 0.142$, $p = 0.432$), or sun rise ($r = -0.302$, $p = 0.088$).

As expected, the animals started activity later with later sun set ($r = 0.600$, $p < 0.000$) and later end of astronomical twilight ($r = 0.598$, $p < 0.000$), as well as on warm (TA max: $r = 0.754$, $p < 0.000$) and rainy days ($r = 0.620$, $p < 0.000$). The end of activity did not correlate significantly with sun rise ($r = -0.02$, $p = 0.904$) nor with 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 sunset ($r = -0.292$, $p = 0.099$), sunrise (0.323 , $p = 0.67$), or even night length ($r = 0.299$, $p = 0.090$), 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 to be expected, evening and morning peak times (EPT, MPT), the peak-to-peak interval (PPI), evening peak height (EPH) and morning peak duration (MPD) were significantly positive or negative correlated with the times of sun set, sun rise, evening end and morning onset of astronomical twilight, as well as with ambient temperature ($p = 0.002$ each). On the other hand, the duration of the evening bout of activity (EPD) did not correlate with any of these parameters, nor the height of the morning activity peak (MPH) correlated with ambient temperature. The parameters EPT ($r = 0.361$, $p = 0.039$), MPT ($r = -0.44$, $r = 0.01$), and the PPI ($r = -0.371$, $p = 0.033$) showed slight co-variation with precipitation, while the EPH and MPD were high significantly negative or positive 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 evening and morning peak height (EPH: $r = -0.546$, $p = 0.001$; MPH: $r = -0.540$; $p = 0.001$), but not with the duration of the evening peak (EPD: $r = 0.104$, $r = 0.566$) and only slightly with that of the morning peak (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 (2100h-0600h), they showed, on average, twice as much motor activity than during the day (0900-1800h). However, the monkeys usually started their nocturnal activity well before sunset and terminated it considerably after sunrise. 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 18:00-21:00 and 06:00-09:00.

Although more daytime activity has been reported in previous studies of this species (Arditi 1992; Fernandez-Duque 2003; Rotundo et al. 2000), this difference is mainly due to differing definitions of day and night time. 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 (2100-0600h and 0900-1800h), as well as the two twilight periods (1800-2100 and 0600-0900).

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 (Fernandez-Duque 2003; Wright 1989), even with the help of night vision goggles, will obviously tend to underestimate the frequency and nature of activity at night.

Alternatively, 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 moonphase. 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. lemurinus griseimembra* recorded in Colombia under natural lighting conditions (Erkert 1974; Erkert 1976). Field observations in Peruvian and Bolivian owl monkeys then indicated increased nocturnal motor and vocalization activity on full moon nights (Aquino and Encarnación 1986; Garcia and Braza 1987; Garcia and Braza 1993; Wright 1978; Wright 1989). Strong moon light 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 only been reported from the activity recordings carried out in 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 to analyse 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. lemurinus griseimembra* (Erkert 1974; Erkert and Groeber 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. lemurinus griseimembra*. These monkeys engaged in maximal activity when exposed to artificial 12:12 h light-dark cycles (LD 12:12) 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 Groeber 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 an LD 12:12, 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-Jaeger 1983).

Despite a predominantly nocturnal activity rhythm, *A. a. azarai* also showed a considerable amount of activity during the bright portion of the 24-h day. Their motor activity was not evenly distributed over the 24-h 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 hours before sunset and after sunrise when luminosity may reach or exceed 500-1000 lx. As

observed in previous studies (Fernandez-Duque 2003), daytime activity levels were highest and lowest following new and full moon nights, respectively (Figure 5). This result may indicate that the monkeys' day time 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., this volume). For example, although *A. a. boliviensis* is nocturnal in Bolivia (Garcia and Braza 1993, 1987), 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 unambiguously define 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 what would have resulted if the times of sunset and sunrise 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 active at various periods during the night, as during the hours of daylight” (Tattersall 1987, p 201). 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 sunset and sunrise, or to the times of the end and beginning of civil, nautical, or astronomical twilight. In chronobiology, the times of sunset and sunrise have usually been chosen as reference phases of the natural light-dark cycle (Daan and Aschoff 1975; Erkert 1974; Erkert 1976; Erkert and Kappeler 2004). To avoid confusion and obtain comparable data in the future, we propose to use the more “classic” reference times of sunset and sunrise.

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(Zoological Society of San Diego) and an Assistant Researcher at the CECOAL (CONICET, Argentina). All aspects of the research conformed to local and international regulations regarding the ethical treatment of animals.

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

Name	Sex	Estimated		Recording
		Age (yrs)	Group Size	period (mo)
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

Table 2. Comparison of average total activity per day at the four phases of the moon. Results of Wilcoxon tests for significant differences between moon phases. N = 7 individuals, n = 33 lunar cycles.

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

Legends

Figure 1. Annual variation of monthly (30 d) 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, hatched bars) at Estancia Guaycolec, Formosa, Argentina.

Figure 2. Top: Double plot of original activity recordings in a male *Aotus azarai azarai* over a period of three 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 night time activity and that around new moon 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.

Bottom: Double plotted bimodal activity pattern of this owl monkey as averaged over the whole recording period shown above. During the night time from 21:00 – 06:00 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).

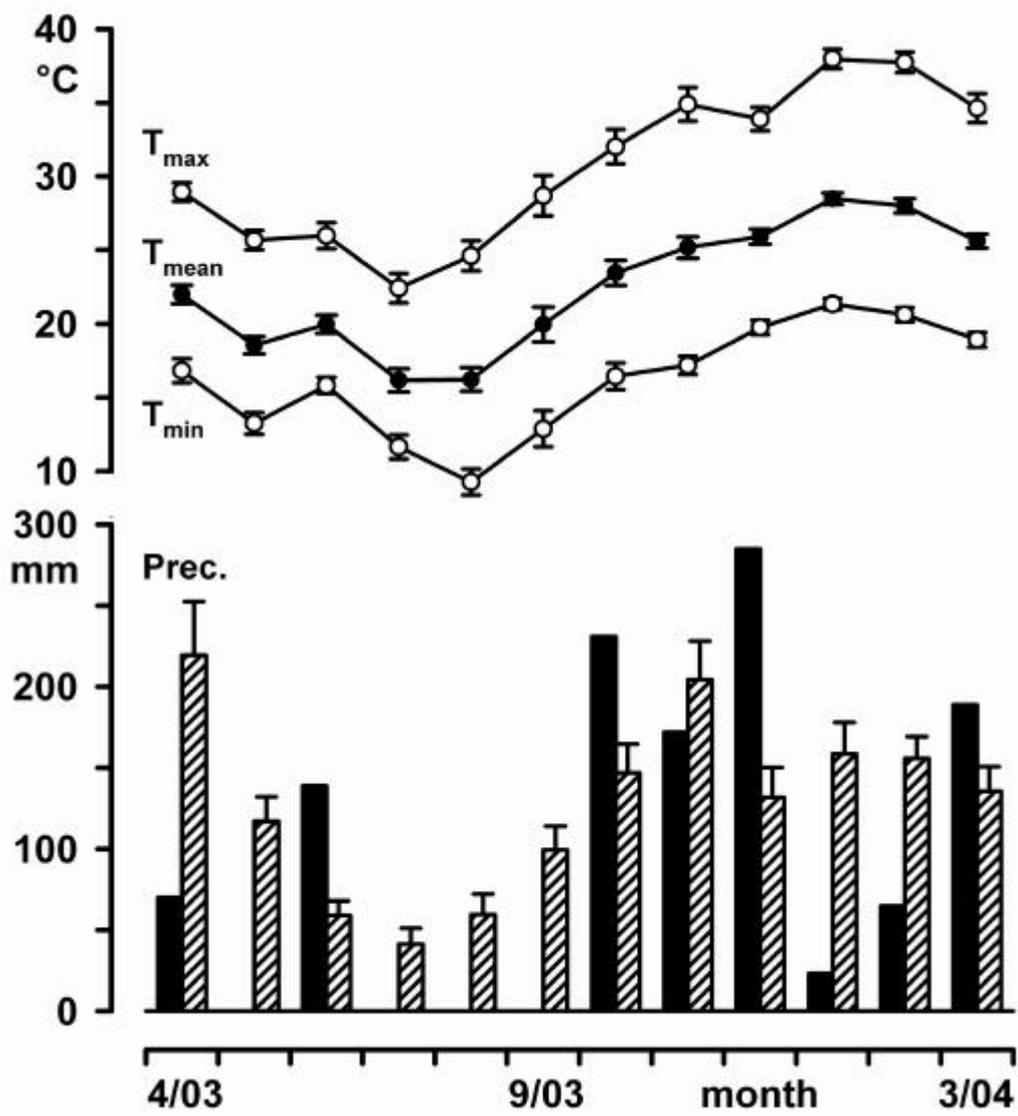
Figure 3. Lunar periodic variation of the activity pattern in wild *Aotus azarai azarai* (N = 5 individuals, n = 23 lunar cycles during five short-day months from April to September) as indicated by the relative amount of activity developed in successive 3-h periods at the four phases of the moon.

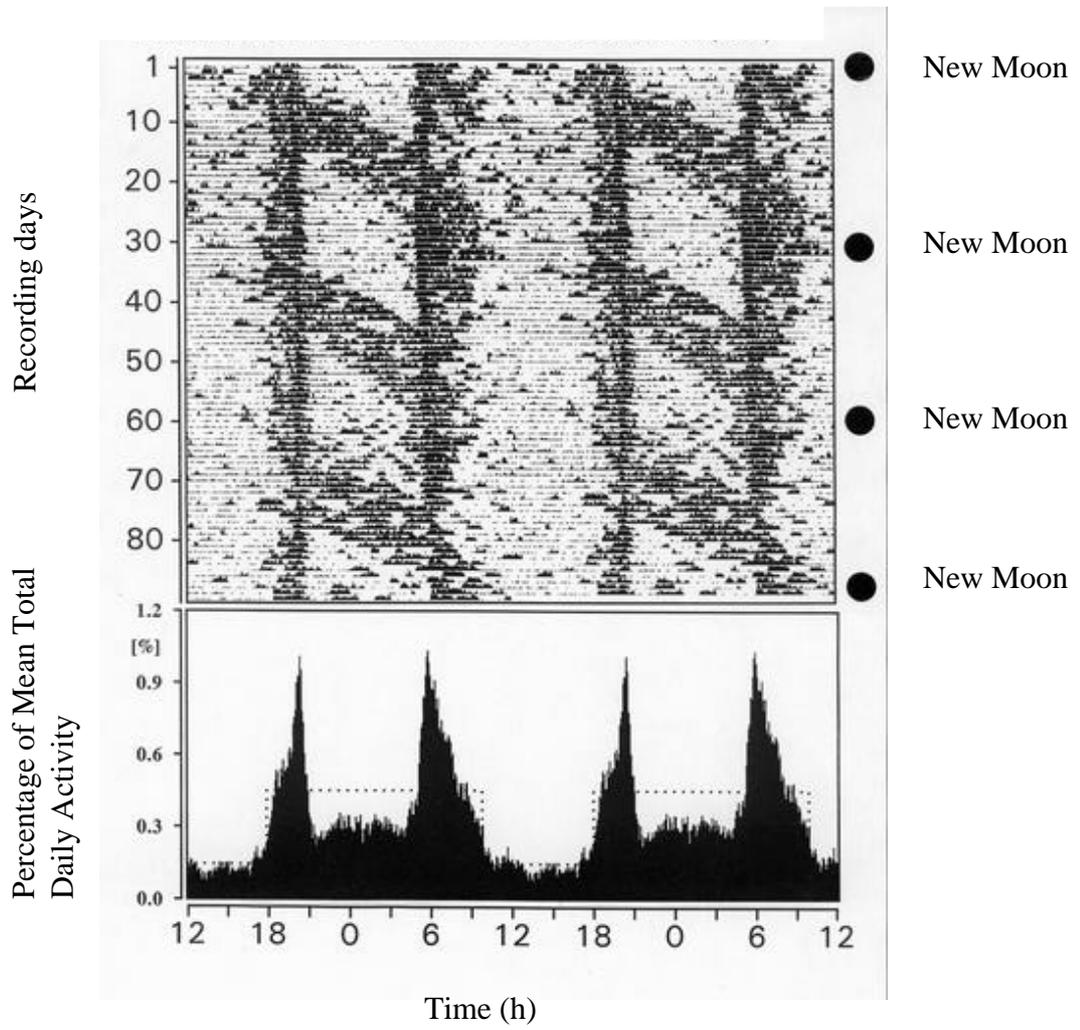
Figure 4. Average amount of total activity per day in thousand counts per day (kc/d + SE) at new, waxing, full, and waning moon (black bars from left to the right; N = 7 individuals, n = 33 lunar cycles).

Fig. 5. Lunar effects on the relative amount of motor activity (% of 24-h total) produced during the bright hours of the day from 0900 to 1800 (top panel) and during the night from 2100 to 0600 (lower panel).

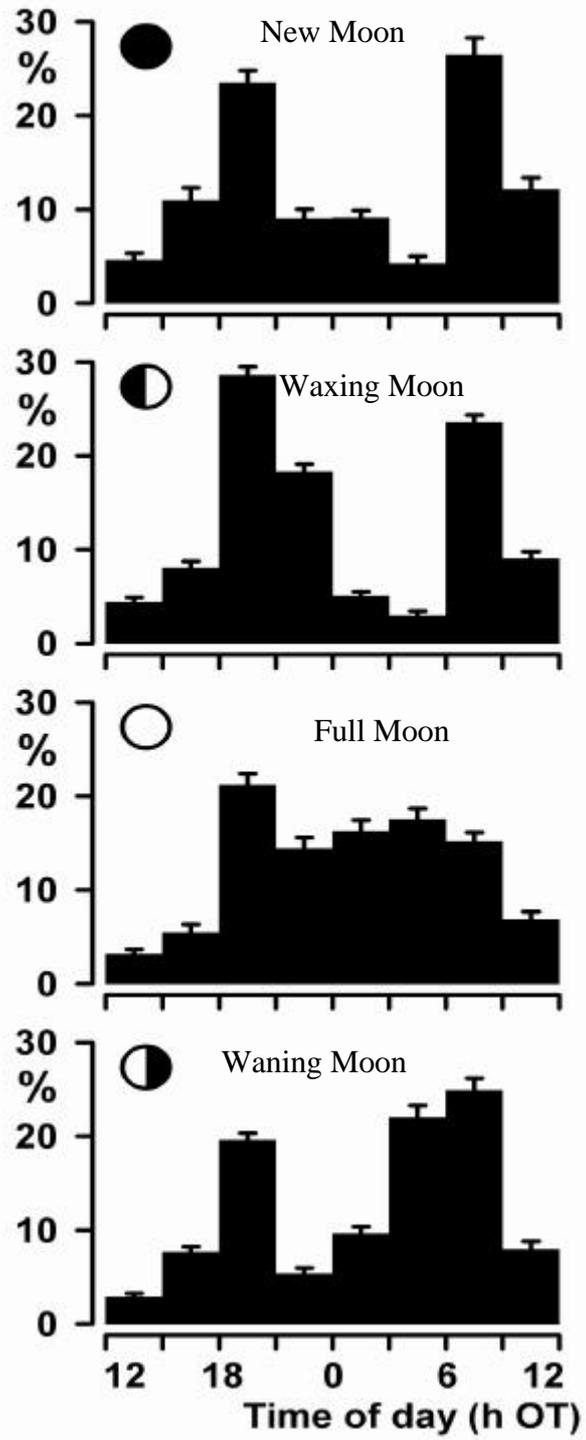
Figure 6. Seasonal variation in the relative amount of activity produced during the bright hours of the day from 09:00-18:00. Mean values as averaged over the data for the four phases of the moon (c.f. Fig. 5, top; N = 5 individuals for the short day lunar months from April/May to September/October, and 2 individuals for the long day lunar months from September/October to March/April of the year).

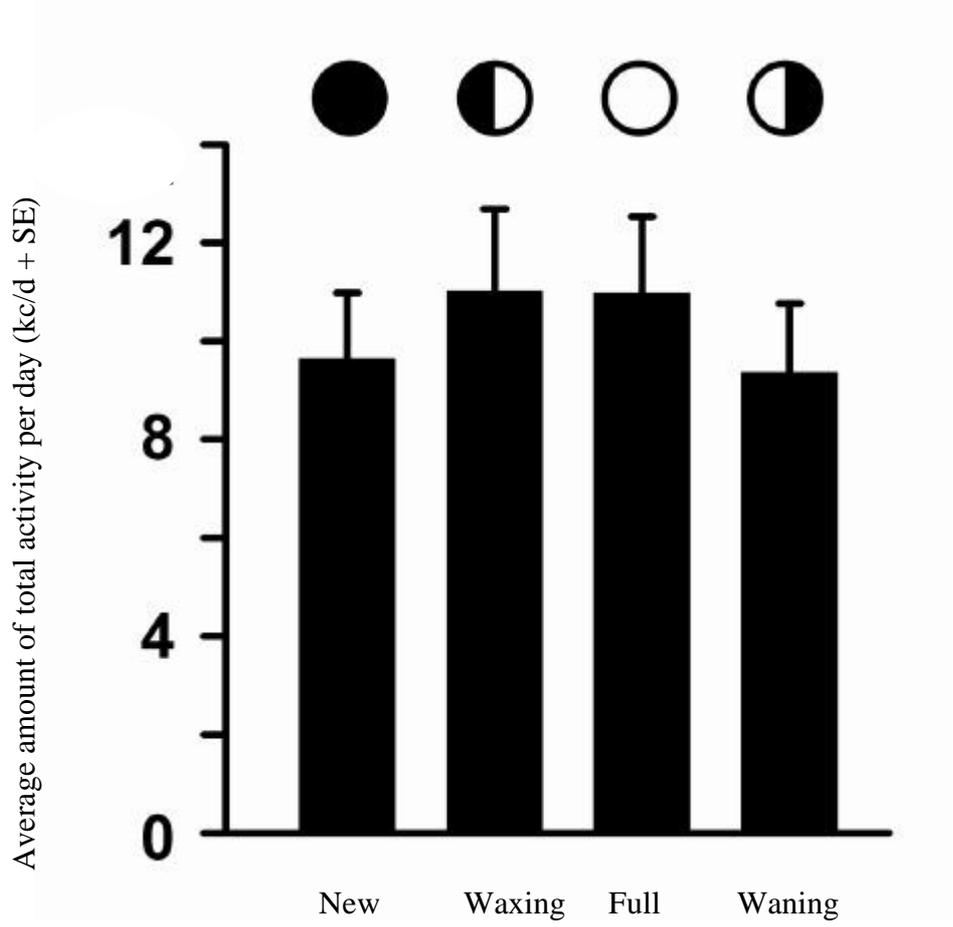
Figure 7. Annual variation of onset and end of activity (AO, AE; black circles and squares) and of evening and morning peak time (EPT, MPT; open circles and squares) of the average monthly activity pattern (arithmetic means \pm SE) in wild *Aotus a. azarai* in relation to the corresponding mean times of sunset and sunrise (SS, SR; solid curves), and the corresponding mean times of end and onset of astronomical twilight (eAT, oAT; broken curve). Ordinate values from top to bottom represent the data for successive calendar months. N=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.

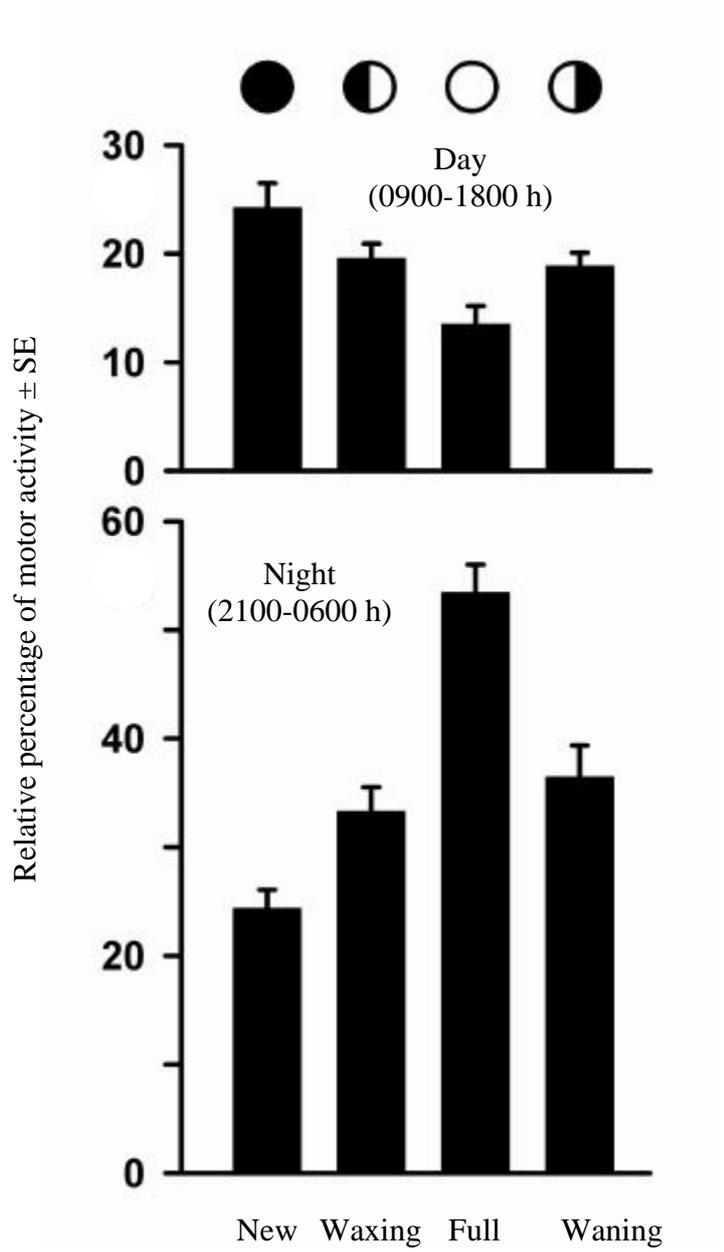




Mean percentage of overall activity per day + SE







Relative amount of activity \pm SE

