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Seasonal Variation of Temporal Niche in Wild Owl Monkeys (*Aotus azarai azarai*) of the Argentinean Chaco: A Matter of Masking?

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Among the more than 40 genera of anthropoid primates (monkeys, apes, and humans), only the South American owl monkeys, genus *Aotus*, are nocturnal. However, the southernmostly distributed species, *Aotus azarai azarai*, of the Gran Chaco may show considerable amounts of its 24-h activity during bright daylight. Due to seasonal changes in the duration of photophase and climatic parameters in their subtropical habitat, the timing and pattern of their daily activity are expected to show significant seasonal variation. By quantitative long-term activity recordings with Actiwatch AW4 accelerometer data logger devices of 10 wild owl monkeys inhabiting a gallery forest in Formosa, Argentina, the authors analyzed the seasonal variation in the temporal niche and activity pattern resulting from entrainment and masking of the circadian activity rhythm by seasonally and diurnally varying environmental factors. The owl monkeys always displayed a distinct bimodal activity pattern, with prominent activity bouts and peaks during dusk and dawn. Their activity rhythm showed distinct lunar and seasonal variations in the timing and daily pattern. During the summer, the monkeys showed predominantly crepuscular/nocturnal behavior, and a crepuscular/cathemeral activity pattern with similar diurnal and nocturnal activity levels during the cold winter months. The peak times of the evening and morning activity bouts were more closely related to the times of sunset and sunrise, respectively, than activity-onset and -offset. Obviously, they were better circadian markers for the phase position of the entrained activity rhythm than activity-onset and -offset, which were subject to more masking effects of environmental and/or internal factors. Total daily activity was lowest during the two coldest lunar months, and almost twice as high during the warmest months. Nighttime (21:00–06:00 h) and daytime (09:00–18:00 h) activity varied significantly across the year, but in an opposite manner. Highest nighttime activity occurred in summer and maximal daytime activity during the cold winter months. Dusk and dawn activity, which together accounted for 43% of the total daily activity, barely changed. The monkeys tended to terminate their nightly activity period earlier on warm and rainy days, whereas the daily amount of activity showed no significant correlation either with temperature or precipitation. These data are consistent with the dual-oscillator hypothesis of circadian regulation. They suggest the seasonal variations of the timing and pattern of daily activity in wild owl monkeys of the Argentinean Chaco result from a specific interplay of light entrainment of circadian rhythmicity and strong masking effects of various endogenous and environmental factors. Since the phase position of the monkeys' evening and morning activity peaks did not vary considerably over the year, the seasonal change from a crepuscular/nocturnal activity pattern in summer to a more crepuscular/cathemeral one in winter does not depend on a corresponding phase shift of the entrained circadian rhythm, but mainly on masking effects. Thermoregulatory and energetic demands and constraints seem to play a crucial role. (Author correspondence: hans.erkert@t-online.de)

Keywords: Activity rhythm, *Aotus*, Cathemeral, Circadian rhythm, Dual-oscillator model, Entrainment, Lunar periodicity, Masking, Natural environment, Primates

INTRODUCTION

Mammals have occupied a diversity of temporal niches that range from strict nocturnal to strict diurnal behavior, with a broad continuum in between (Curtis & Rasmussen, 2006; Refinetti, 2006, 2008). Among primates, most strepsirrhine (wet-nosed) prosimians are strictly nocturnal. Only some Madagascan lemurids are diurnal, and a few others have recently been identified as "cathemeral," being active both during the night and day (Curtis & Rasmussen, 2006; Tattersall, 1987, 2006). In contrast, all but one of the 40 genera of haplorrhine (dry-nosed) anthropoid primates (monkeys, apes, and humans) are

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diurnal. Only the South American owl monkeys of the genus *Aotus* show nocturnal habits (Fernandez-Duque, 2011; Wright, 1989). However, the southernmostly distributed species *Aotus azarai azarai*, which is found from southern Bolivia to the northern Argentinean Chaco, may show considerable amounts of its 24-h activity during bright daylight (Fernandez-Duque, 2003; Wright, 1989).

The cathemeral behavior of this owl monkey species is closely related to the lunar light cycle (Fernandez-Duque, 2003; Fernandez-Duque & Erkert, 2006; Fernandez-Duque et al., 2010). On days around full moon, animals display significantly more nocturnal activity than on days around new moon, when more activity is shifted into the daytime. Increased diurnality has also been linked to changes in ambient temperature and other environmental factors that vary throughout the year (Fernandez-Duque, 2003; Fernandez-Duque & Erkert, 2006). Since the seasonal variations in some of these factors are indeed significant in the subtropical Argentinean Chaco, it is expected that the owl monkeys living there will exhibit seasonal changes in the daily distribution of locomotor activity, including the ratio of nighttime: daytime activity.

Laboratory studies have shown that regulation of daily activity and body temperature rhythms in Colombian owl monkeys (*Aotus lemurinus griseimembra*) is achieved by a precise circadian timing system (Erkert & Thiemann, 1983; Hoban et al., 1985; Rappold & Erkert, 1994; Rauth-Widmann et al., 1991). Because the period of the circadian oscillation produced in the central nervous pacemaker in the suprachiasmatic nuclei (SCN) deviates from 24 h, the circadian clock must be phase-set daily to the environment's 24-h periodicity. In owl monkeys, like in most species, the 24-h light-dark (LD) cycle is the predominant zeitgeber or entraining agent (Albers et al., 1984; Erkert & Thiemann, 1983; Rappold & Erkert, 1994; Rauth-Widmann et al., 1991). As a result of this photic entrainment of the circadian timing system, the animals' activity rhythm maintains a relatively stable phase relationship with the prevailing LD cycle (Daan & Aschoff, 1975, 2001; Johnson et al., 2003). This phase-angle difference (ψ) is usually measured as the time between specific phase markers of the circadian rhythm, such as the onset or offset of the daily activity time, and an arbitrarily chosen reference point of the zeitgeber, such as the times of lights-on and lights-off or of sunrise and sunset, respectively. The phase-angle difference depends on the species' free-running period (τ) and the species-specific phase-shift responses to changes in light intensity, which are portrayed by the phase response curve (Daan & Aschoff, 2001; Daan & Pittendrigh, 1976; Johnson et al., 2003; Pittendrigh & Daan, 1976). Additionally, the phase-angle difference will systematically change with some zeitgeber parameters, such as its period (T) and amplitude (maximum-minimum difference), respectively, and photoperiod, namely, the relative duration of photophase to the scotophase of the entraining LD cycle. Of these parameters, both the period and the large difference of lowest nighttime to highest daytime luminosity (corresponding to $\sim 5 \times 10^{-4}$:10^5 lux at new moon with a clear sky) of the more or less trapezoidal natural LD cycle remain relatively constant throughout the year over a wide range of latitudes. At the study site, the duration of evening and morning astronomical twilight also does not vary considerably over the year (76–91 min). Thus, it is mainly the seasonal variation in photoperiod, i.e., duration of the solar day from sunrise to sunset, which, at the relatively high latitude of the North Argentinean Chaco, varies as much as 3.25 h over the year that is expected to primarily affect the distribution of activity of owl monkeys throughout the 24-h day. However, light, ambient temperature, relative humidity, food availability, and social contact may also acutely influence circadian outputs through direct enhancing or inhibitory effects. These "masking effects" modify circadianly programmed physiological and behavioral processes (Aschoff et al., 1982; Erkert & Groeber, 1986; Mrosovsky, 1999). Hence, the seasonal variation of those factors can also contribute to seasonal variation in the activity pattern of owl monkeys living in their natural environment.

Previous observational studies of the owl monkey population inhabiting gallery forests in Formosa Province of Argentina focused on behavioral ecology (Fernandez-Duque, 2003, 2009, 2011; Fernandez-Duque & Rotundo, 2003; Fernandez-Duque et al., 2002; Rotundo et al., 2005) and moonlight effects on activity patterns (Fernandez-Duque & Erkert, 2006; Fernandez-Duque et al., 2010). Here, we present the results of a study that assessed the seasonal variation in the temporal niche of this southernmostly distributed owl monkey subspecies that would result from entrainment and masking of circadian rhythms by the seasonally and diurnally varying environmental factors of the Argentinean Chaco. For that purpose, we carried out long-term activity recordings (3–6 mo each) on 10 wild owl monkeys between 2003 and 2006.

In reality, entraining and masking effects of environmental factors on circadian rhythms can reliably be differentiated only through specific laboratory experiments. Theoretically, it is not possible to discriminate between circadian entrainment and masking by environmental factors in wild-living animals. However, in the case of the wild owl monkeys of the Argentinean Chaco, comprehensive knowledge of its behavioral ecology based on field studies of this species plus chronobiological laboratory experiments on a closely related species, which included thorough analyses of the entraining and masking effects of light and ambient temperature (for review see Erkert, 2008), constituted optimal background for a sound chronobiological analysis of the circadian and masking components determining the activity pattern of wild owl monkeys.

METHODS

Study Area and Subjects

The study area is located in the gallery forests along the Riacho Pilagá, a tributary of the Río Paraguay. The area

TABLE 1. Individual owl monkeys fitted with Actiwatch AW4 collars during the various lunar months from March 2003 to April 2006

Lunar month no.	2003	2004	2005	2006	Total	Males, females
1		An, Fa	An, Fa, Ce	Du, Er	7	7, 0
2		An, Fa	An, Fa, Ce	Du, Er	7	7, 0
3	Ir, Vi, Fu	Fa	Fa	Du, Er	7	5, 2
4	Ir, Vi, Fu, Eu	An	Fa	Du, Er	8	5, 3
5	Ir, Vi, Fu, Eu	An, Fa, Ce			7	4, 3
6	Ir, Vi, Fu, Eu, Pa	Fa, Ce			7	4, 3
7	Ir, Vi, Fu, Eu, Pa	Fa, Ce			7	4, 3
8	Ir, Vi, Eu, Pa	Fa, Ce			6	4, 2
9	An	Fa, Ce			3	3, 0
10	An	An, Ce			3	3, 0
11	An, Fa	An, Fa, Ce			5	5, 0
12	An, Fa	An, Fa, Ce	Du, Er		7	7, 0
Total	31	25	10	8	74	58, 16

Subject abbreviations: An: Anacleto; Ce: Cesar; Du: Durazno; Eu: Eulogia; Er: Erico; Fa: Fabian; Fu: Fumata; Ir: Irene; Pa: Pampero; Vi: Victor.

belongs to Estancia Guaycolec, a cattle ranch located 25 km from the city of Formosa in the Argentinean portion of the South American Gran Chaco (58°11′W, 25°58′S, 60 m above sea level [asl]). This subtropical region is characterized by pronounced seasonality in photoperiod, ambient temperature, precipitation, and food productivity (Fernandez-Duque & Erkert, 2006; Fernandez-Duque et al., 2002; Van der Heide et al., 2011). Between March 2003 and April 2006, 9 males and 10 females were caught and provided with an activity recording collar containing an Actiwatch AW4 (Cambridge Neurotechnology, Cambridge, UK) motion logger. Recording collars were fitted three times in each of two animals (Fa, An) and twice in another one (Ce) (Table 1). Because owl monkeys are socially monogamous (Fernandez-Duque, 2011), the pairmates of the individuals wearing an AW collar were fitted with a radio collar to facilitate relocating the social groups and recapture of the animals wearing an AW collar. However, three males and three females fitted with AW collars were evicted from their group by same-sex intruders and disappeared. One male and one female had to be recaptured after only 1 wk, and their collars removed, since they had also been evicted from their groups. Finally, the data from two other females could not be downloaded because of malfunctioning actimeters. Due to these problems, usable activity records were obtained only from 10 of the owl monkeys initially fitted with AW collars (Table 1).

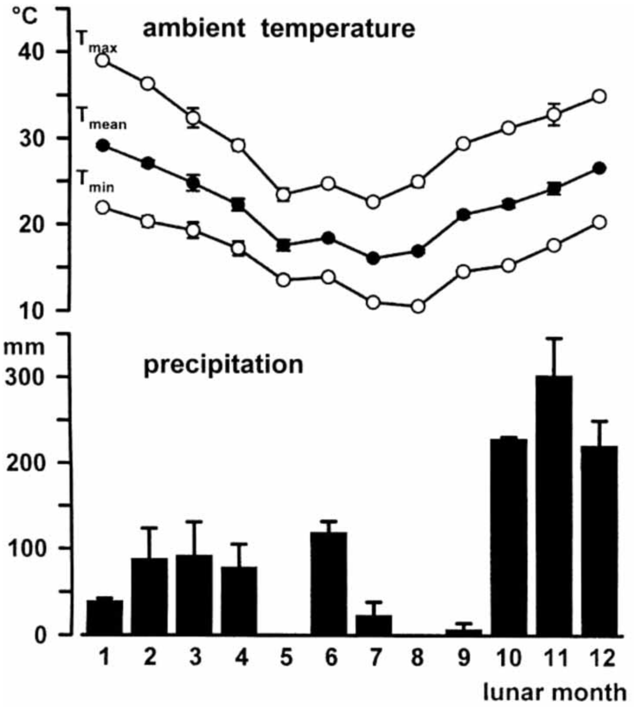

FIGURE 1. Average +/− SEM lunar monthly ambient temperature (daily maxima, means, minima) and average (+ SEM) precipitation at the study site in Formosa, Argentina, from March 2003 to April 2006. In order to achieve comparability to Figures 2–10, data were weighted according to the number of individuals subjected to the respective conditions.

Precipitation, Temperature, and Astronomical Data

Precipitation and temperature data were collected daily throughout the 3 yrs of the study. Precipitation records were obtained from Estancia Guaycolec, and summarized over lunar months. Ambient temperature (Ta) was measured hourly with a Stowaway XTI data logger positioned at the entrance of the study area, and daily minimum, mean, and maximum temperatures were averaged over lunar months. When preparing Figure 1, in order to establish direct comparability with the other figures, the lunar monthly averages of ambient temperature and precipitation were weighted according to the number of the recorded monkeys subjected to them. The local times of sunset and sunrise, beginning and end of astronomical twilight, and the dates of full-moon and new-moon days were obtained from the Web site of the US Naval observatory (http:aa.usno.navy.mil/data).

Procedures

In order to fit the recording collars containing an Actiwatch AW4 accelerometer/datalogger device (Cambridge

Neurotechnology), individuals were captured using darts with small doses of ketamine hydrochloride (50 mg/kg; Vetanarcol, Konig, Argentina; Fernandez-Duque & Rotundo, 2003). Captured animals first underwent a thorough physical examination; then, samples for genetic analyses were taken, and finally the collars fitted. The collared animals were released close to their social groups and observed until they had rejoined them. Table 1 summarizes the data on subjects and recording periods that are evaluated and discussed here.

The Actiwatch AW4 devices were programmed to record and store activity data at 5-min intervals. After periods ranging from 3 to 6 mo, the animals were recaptured and the data downloaded to a personal computer (PC) using the Actiwatch/Sleepwatch program (Cambridge Neurotechnology). Data file headings were then edited for our own PGRAPH program used to create double-plots of the original data (cf. Figure 2, top), calculate 5-min or 1-h average lunar monthly activity patterns (cf. Figure 2, bottom), and carry out periodogram analyses according to Doerrscheid and Beck (1975).

To control for the effects of moonlight on activity, we determined the individuals' mean activity patterns across lunar months instead of calendar ones. Thus, the data were organized in periods of lunar cycles going from one full-moon day at 12:00 h to the following full-moon day at 12:00 h. In this manner, the 10 subjects contributed activity data from a total of 74 lunar cycles, although the 12 lunar months of the year were not sampled in a fully balanced manner (Table 1). To test for seasonal variation in the pattern and timing of activity, we first calculated each individual's lunar monthly mean activity pattern using the recorded 5-min values. In order to compensate for interindividual differences in the activity level, and/or for differences in the AWs' sensitivity, the subjects' averaged 5-min values are given as percentage of the respective lunar months' average total activity/d. To further evaluate/check seasonal variation, we also compared the data from the summer half year (lunar months 10–3) with those from the winter half year (lunar months 4–9; cf. Table 3).

As parameters of the monkeys' pronounced bimodal average lunar monthly activity patterns (Figure 2), we determined the time of activity-onset and -offset, the duration of the evening (E) and morning (M) activity bouts, and the time and height of the E and M activity peaks. The latter were defined as the highest 5-min values of the E and M activity bouts. The average

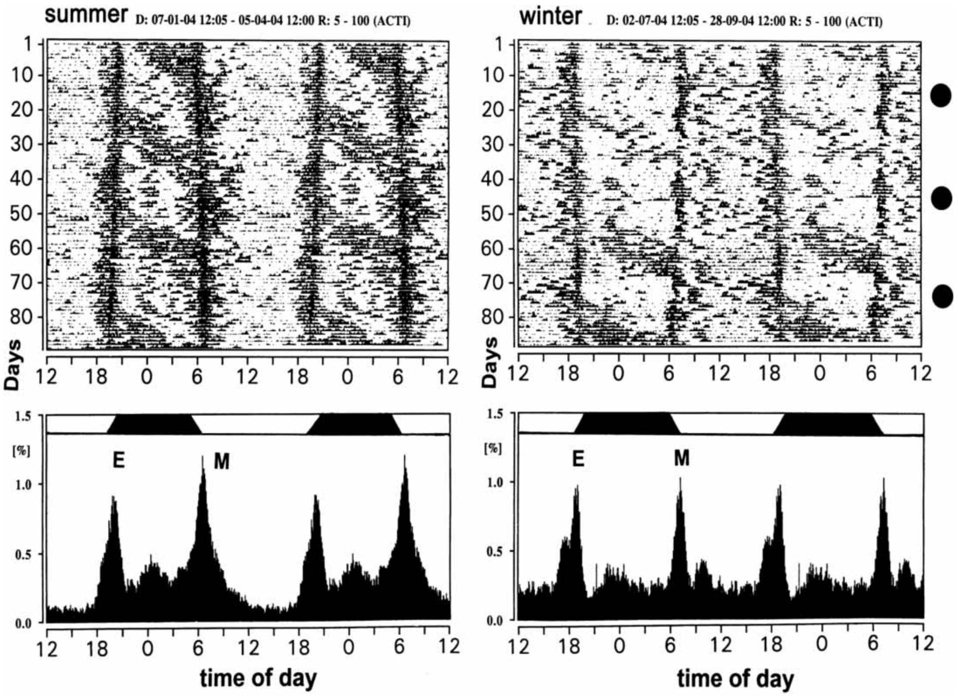

FIGURE 2. (Top) Original activity records (double-plotted) from a wild male *Aotus azarai azarai* (Fa) of the Argentinean Chaco during three lunar months (full moon to full moon) of the warm long-day (left panels) and the cold short-day (right panels) halves of the Austral year. Note that the nocturnal activity course of the monkey's locomotor activity is modulated by the lunar periodicity; around new-moon days (indicated by black dots on the right margine) both in the evening and the morning more activity is shifted into the bright part of the day, and that more daytime activity is shown throughout the short-day than long-day months. Drawn are 5-min values with the line spaces corresponding to 5–100 counts/5-min bin. Abscissa: Time-of-day in hours. Ordinate: successive days from top to bottom. (Bottom) Double-plotted activity patterns obtained by averageing over of the data sets shown in the upper panels. While the long-day activity pattern (left) is characterized by a higher activity level at night, the short-day pattern (right) shows an almost equal activity level during night and day. Ordinate: Relative activity/5-min bin in % of average daily total activity. Bars on top of the panels correspond to the respective average solar day (completely open parts), astronomical night (completely black parts), and durations of astronomical twilights (parts with increasing and decreasing black and white portions). E and M indicate the evening and morning activity peaks, respectively.

monthly nocturnal activity minimum (trough height) was taken as an estimate for the depth of the nightly resting period interposed between the E and M activity bouts. Additional parameters were the duration of the nocturnal activity time from the onset of the E activity bout to the end of the M activity bout, the interval between the E and M activity peaks (peak-to-peak interval), and the phase-angle differences of the onset and offset of nocturnal activity (ψ_o, ψ_e), and of the E and M activity peaks. The reference phase for calculating the phase-angle difference of E activity-onset and E peak was sunset, and for M activity-offset and M peak it was sunrise. To test for seasonal variation in crepuscular, nighttime, and daytime activity, relative proportions of activity for the periods 18:00–21:00, 21:00–06:00, 06:00–09:00, and 09:00–18:00 h were calculated using 1-h activity patterns. All time-related parameters were measured as the number of 5-min bins that passed from the chosen reference time (12:00 h) to sunset, sunrise, onset and offset of activity, and times of the E and M activity peaks, or as the number of 5-min bins between two time parameters. Activity-onset was defined as the number of 5-min bins that passed from 12:00 h until before the E peak, the first of a series of more than four 5-min mean values occurred that exceeded the 24-h average 5-min activity level of .35%. Accordingly, the offset of M activity and the end of the E activity bout corresponded to the last one of a series of four 5-min bins that exceeded the .35%-average after the M or E peak, respectively. Corresponding procedures were used to determine the beginning of the M activity bout. In order to estimate the effects of certain environmental factors on the owl monkeys' lunar monthly average pattern and timing of activity, these parameters were correlated with the respective lunar monthly averages of astronomical and temperature data and with the corresponding lunar monthly amount of precipitation, respectively. Daytimes are given in Argentinean official time, which, at the study site, is phase advanced in relation to local time by more than 1 h. Averages are given as arithmetic means ± standard error of the mean (SEM).

Statistical Analyses

SPSS (formerly SPSS Inc., Chicago/USA, now IBM Corp., Armonk/USA), SigmaStat, and SigmaPlot (Systat Software Inc., San José/USA) were used for statistical analyses and graph creation, respectively. Post hoc statistical analyses were carried out as appropriate with one-way or mixed-model analyses of variance (ANOVAs) followed by Scheffé tests, with Pearson's correlation analysis, or with nonparametric Friedman, Wilcoxon, or 2 × 2 chi-square tests (Weber, 1972). $p \leq .05$ was considered to indicate statistically significant differences or correlations.

Ethical Standards

All procedures were performed following protocols approved by the animal care committee (IACUC) at the Zoological Society of San Diego and Argentinean authorities. The experimental protocol conforms to the international ethical standards as outlined in Portaluppi et al. (2010).

RESULTS

General Daily Activity Patterns

The AW4 accelerometers recorded the owl monkeys' locomotor activity very precisely. As an example, the upper panels of Figure 2 show double-plotted 5-min-binned actograms of a single male owl monkey (Fa) during three warm long-day lunar months (left) and three cold short-day lunar months (right) of the Austral year. This individual, like all others, was most active around dusk and dawn, as well as throughout the moonlit parts of the night. The moonlight-related nocturnal activity, which should not be mistaken for a free-running circadian component, as well as the advanced onset of E activity and the delayed offset of M activity observed on days around new moon indicate a pronounced lunar periodic variation in the daily pattern and timing of activity. Moreover, the elevated daytime activity and a less pronounced lunar periodic variation of nocturnal activity during the short-day winter months (right) indicate a clear seasonal variation in some parameters of the owl monkeys' activity rhythm. Accordingly, this individual's activity pattern shows a predominantly crepuscular/nocturnal behavior during the summer and a crepuscular/cathemeral pattern with similar diurnal and nocturnal activity levels during the cold winter months (Figure 2, bottom panels). All individuals showed a similarly distinct bimodal activity pattern with pronounced activity peaks during dusk and dawn, and a much higher activity level throughout the night than during daytime (Figure 3).

Timing of Activity

Throughout the year, almost half (43%) of the total daily activity of the owl monkeys was recorded during the crepuscular periods corresponding to the E (18:00–21:00 h) and M activity bouts (06:00–09:00 h). The monkeys' onset of activity at dusk varied in close relation to the time of sunset, whereas its offset in the morning did not show a correspondingly clear relationship to sunrise (Figure 4). On average, the onset of nocturnal activity preceeded sunset by ≈1 h (59.7 ± 34.5 min; Wilcoxon test, $p < .001$), whereas the activity-offset at dawn occurred more than 1 h after sunrise (78.6 ± 56.3 min; Wilcoxon test, $p < .001$). The E and M activity peaks were even more tightly linked to sunset and sunrise (Figures 4, 5). The E peak was, on average, .5 h phase-delayed relative to sunset (33 ± 15 min; Wilcoxon test, $p < .001$) and showed a stronger positive correlation with sunset ($r = .921$, $p < .001$) than acvtivity-onset ($r = .731$, $p < .001$). Likewise, the M activity peak, which was usually slightly phase-advanced relative to sunrise (+16.2 ± 15.1 min; Wilcoxon test, $p < .001$), showed a strong positive correlation with sunrise ($r = .941$, $p < .001$), whereas the offset of activity did not ($r = .095$, $p = .422$). The latter resulted

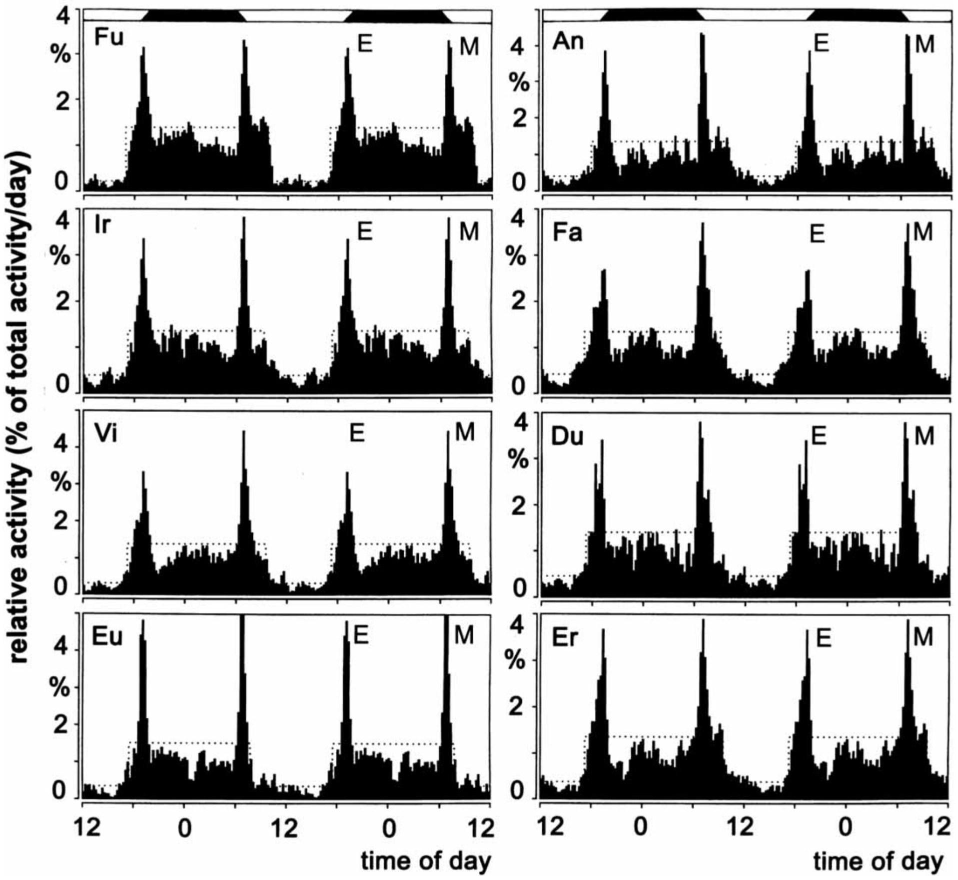

FIGURE 3. Double-plotted average activity patterns (in 15-min bins) of eight individuals of the owl monkey population inhabiting the study site in Formosa, Argentina, throughout the fourth lunar month (cf. Table 1; new-moon to new-moon periods). Whereas the activity patterns shown on the left were recorded concurrently under identical environmental conditions in April/May 2003, the patterns on the right come from recording periods ranging from the end of March to the first few days of May in 2004 (An), 2005 (Fa), and 2006 (Du, Er). Bars on top of the upper panels correspond to the respective average solar day (completely open parts), astronomical night (completely black parts), and durations of astronomical twilights (parts with increasing and decreasing black and white portions). Ordinate: Relative activity/15-min bin in % of average daily total activity. Dotted lines within the diagrams indicate the best-fitting square-wave patterns. E, M: evening and morning activity peaks. For subject abbreviations, see Table 1.

mainly from a markedly later activity-offset from October to January (lunar months 10–1; Figure 5).

The phase position of the E activity-onset and the E activity peak in relation to sunset remained fairly constant through the year. On the other hand, the phase-angle differences of the M activity peak and the M activity-offset showed significant seasonal variations (Figures 5, 6; Table 2). These two findings suggest that the offset of M activity is strongly influenced by environmental parameters (see Discussion). The comparison of the data from the short-day half year with those from the long-day half year yielded similar results (Table 3).

Total Daily Activity

The total daily activity of the owl monkeys changed throughout the year (Figure 6). The lunar monthly averages indicated seasonal variation in the level of locomotor activity, with lowest values during the two coldest lunar months (7, 8), and almost twice as much activity during the warmer lunar months 10–12 (mixed-model [MM]-ANOVA, $F_{(11)} = 4.847$, $p < .001$). The average total daily activity was 31% higher during the six lunar months of the warmer long-day half year than it was during the six short-day lunar months ($\chi^2_{(1)} = 5.33$, $p < .05$).

Activity Pattern

Nocturnal activity time varied seasonally, between 12.2 and 15.4 h. On average, it exceeded by 2.4 ± .8 h the solar night (range: 10.25–13.5 h), whereas the time between the E and M peaks was on average 49 ± 12 min shorter than the solar night. The seasonal variation reached statistical significance for both parameters (Table 2; $p < .001$), but the interval between the E and M peaks was more closely related to night length ($r = .973$, $p < .001$) than the interval between the evening activity-onset and the morning activity-offset ($r = .546$, $p < .001$). Comparison of the data from the short-day half year with those from the long-day half year produced similar results (Table 3).

The height of the E and M activity peaks also varied over the year, with higher values during the winter months (Figure 7, Table 2). The height of the E peak showed a more pronounced seasonal variation than the height of

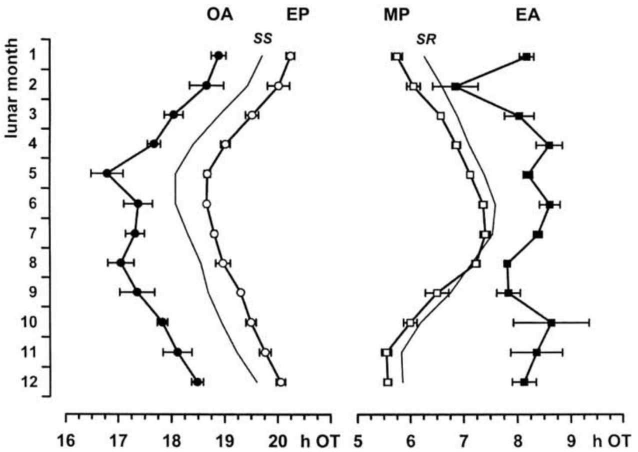

FIGURE 4. Seasonal variation of lunar monthly averages (± SE) of onset and end of activity (AO, AE) and average times (± SE) of evening and morning activity peaks (EP, MP) in relation to sunset (SS, left) and sunrise (SR, right). h OT: Argentinean official time.

the M peak. This was so because the former was significantly higher during the short-day months than during the long-day months, whereas there were smaller differences in the height of the M peak between the short-day and long-day months ($p = .001$ vs. $p = .06$; Table 3). However, comparison of the number of lunar months with a higher M than E activity peak for the long-day half year and for the short-day half year showed a statistically significant difference ($\chi^2_{(1)} = 6.71$, $p < .01$). During the long-day months, the M peak was more than four times as often higher than the E peak (higher M peak:higher E peak = 29:7). Throughout the short-day period, the number of activity patterns with higher M than E peaks roughly corresponded to that of patterns with higher E than M peaks (higher M:higher E peaks = 20:18).

The duration of the E and M activity bouts varied significantly across the year (Table 2). During the relatively long and warm days of the summer half year, the M bouts tended to be longer than the E bouts, whereas during the relatively short and cold days of the winter half year the E activity bout was longer than the M activity bout (Figure 8). The differences between the duration of the two activity bouts reached statistical significance for both half-year periods (Table 3). Throughout the long-day half year, the duration of the M bout exceeded that of the E bout considerably, whereas the relationship was reversed during the short-day half year (Figure 8; $\chi^2_{(1)} = 17.78$, $p < .01$).

The nightly activity minimum (trough height) also showed significant variation across the year (Figure 9; Table 2). Like for total activity/d, the lowest mean value was recorded in the 8th and the highest one in the 11th lunar month. But, contrary to total activity, no significant drop was recorded during the first two lunar months of the year. Throughout the long-day months, the trough height averaged .18% ± .05% of the mean daily total activity, whereas it was only .10% ± .05% during the short-day months (Table 3).

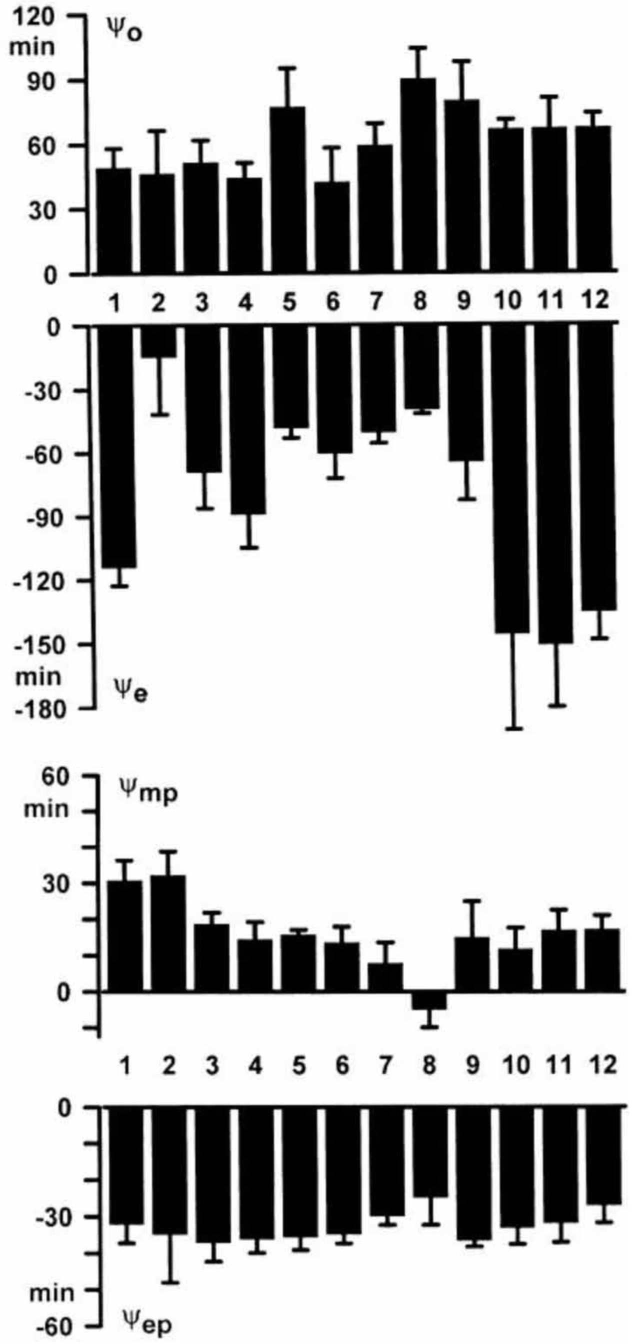

FIGURE 5. (Top) Seasonal variation of average (+ SEM) phase-angle differences of onset (ψ_o) and offset (ψ_e) of the owl monkeys' nocturnal activity time. (Bottom) Seasonal variation of the average (+ SEM) phase-angle differences of the evening and morning activity bouts (ψ_{ep}, ψ_{mp}) across the year. Note the different scales of the ordinates.

Nighttime and Daytime Activity

Both nighttime (21:00–06:00 h) and daytime (09:00–18:00 h) activity showed pronounced seasonal variation, but with an opposite time course (Figure 10; Table 2). Nighttime activity was highest in January (46.6% ± 2.3%) and lowest in August (28.4% ± 3.1%), whereas daytime activity reached its maximum in August (31.2% ± 5.6%) and was lowest in January (13.2% ± 2.2%). During the long-day half year, nighttime activity accounted for

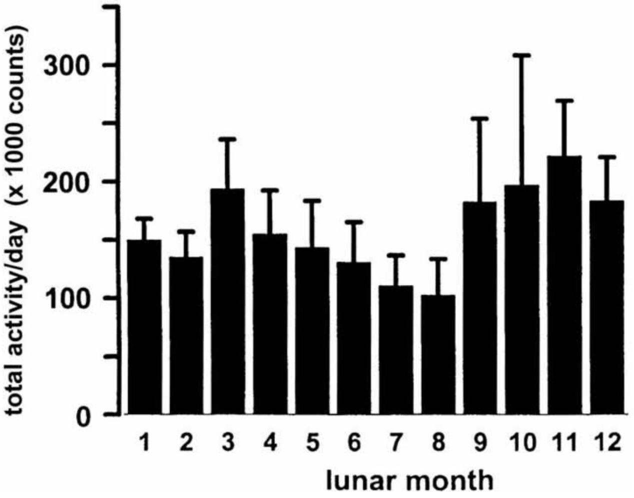

FIGURE 6. Seasonal variation of lunar monthly averages (+ SE) of daily total activity. Abscissa: successive lunar months. Ordinate: Total activity/d (×1000 counts).

TABLE 2. Results of ANOVA testing for seasonal variation in the parameters of activity in wild owl monkeys of the Argentinean Gran Chaco

Parameter	*df*	*F*	*p*
ψ_o	11	1.347	.222
ψ_e	11	7.631	<.001
ψ_{ep}	11	.402	.950
ψ_{mp}	11	3.419	.001
AA	11	.738	.698
EPH	11	1.779	.078
MPH	11	1.075	.396
TH	11	7.713	<.001
NAT	11	7.414	<.001
PPI	11	130.710	<.001
EBD	11	2.666	.007
MBD	11	7.484	<.001
Rel.act.18-21	11	1.223	.292
Rel.act.21-06	11	14.224	<.001
Rel.act.06-09	11	6.179	<.001
Rel.act.09-18	11	7.530	<.001

ψ_o, ψ_e, ψ_{ep}, ψ_{mp}: phase-angle differences of onset and offset of nocturnal activity time (NAT) and of the evening and morning activity peaks (EP, MP) to sunset and sunrise, respectively; AA: average total activity/d; EPH, MPH: height of E and M activity peaks; TH: nocturnal activity minimum; NAT: nocturnal activity time; PPI: interval between evening and morning activity peaks; EBD, MBD: duration of evening and morning activity bouts. Rel. act.: relative activity (% of AA) from hour to hour.

TABLE 3. Results of ANOVA testing for significant differences between the short-day and the long-day half of the year in parameters of activity in wild owl monkeys of the Argentinean Gran Chaco

Parameter	*df*	*F*	*p*
ψ_o	1	.691	.409
ψ_e	1	9.592	.003
ψ_{ep}	1	.067	.797
ψ_{mp}	1	13.144	.001
AA	1	1.577	.213
EPH	1	11.316	.001
MPH	1	3.639	.060
TH	1	46.275	<.001
NAT	1	36.111	<.001
PPI	1	267.417	<.001
EBD	1	15.363	<.001
MBD	1	39.802	<.001
Rel.act.18-21	1	1.030	.314
Rel.act.21-06	1	78.792	<.001
Rel.act.06-09	1	.355	.553
Rel.act.09-18	1	41.223	<.001

ψ_o, ψ_e, ψ_{ep}, ψ_{mp}: phase-angle differences of onset and offset of nocturnal activity time (NAT) and of the evening and morning activity peaks (EP, MP) to sunset and sunrise, respectively; AA: average total activity/d; EPH, MPH: height of E and M activity peaks; TH: nocturnal activity minimum; NAT: nocturnal activity time; PPI: interval between evening and morning activity peaks; EBD, MBD: duration of evening and morning activity bouts. Rel. act.: relative activity (% of average total activity/d) from hour to hour.

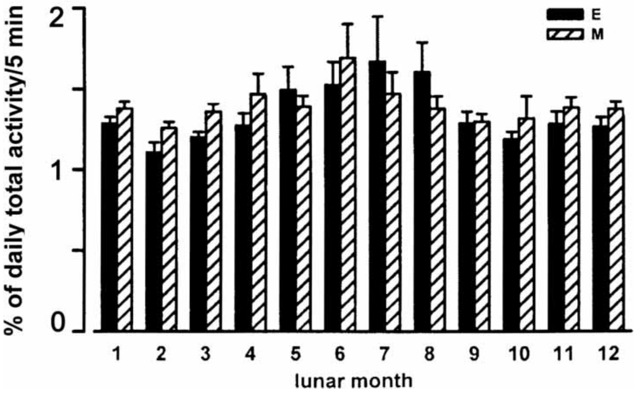

FIGURE 7 Seasonal variation of the average (+ SEM) height of evening (E; black columns) and morning (M; hatched columns) activity peaks.

42% ± 4% of the average daily total activity, whereas the daytime activity was only 15.8% ± 2.3%. Throughout the short-day/long-night months, average nighttime activity decreased to 31.6% ± 3.3%, whereas daytime activity increased to 25.2% ± 4.8%. The differences between nighttime and daytime activity were statistically significant for both the short-day and the long-day halves of the year (Table 3). In contrast, the amount of dusk and dawn activity did not differ much across the year (Figure 9). Dawn activity (06:00–09:00 h) tended to vary slightly more than dusk activity (18:00–21:00 h). Accordingly, its seasonal variation reached statistical significance (Table 2), whereas the variation of dusk activity did not.

Relation of Activity Rhythm Parameters to Environmental Factors

Neither the phase position of activity-onset nor that of the E peak was strongly related to any of the meteorological parameters ($r = -.04$ to $-.211$, $p = .73$ to $.071$). In contrast, the phase of M activity-offset was negatively correlated with the ambient temperature ($r = -.37$ to $-.39$, $p = .001$ each) and precipitation ($r = -.52$, $p < .001$).

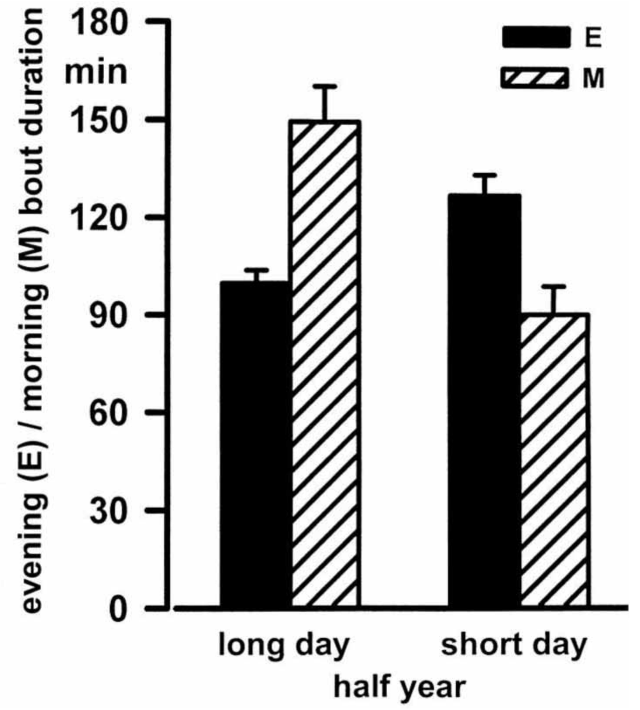

FIGURE 8. Average (+ SEM) lunar monthly duration of evening and morning activity bouts throughout the long-day (left) and short-day (right) half year.

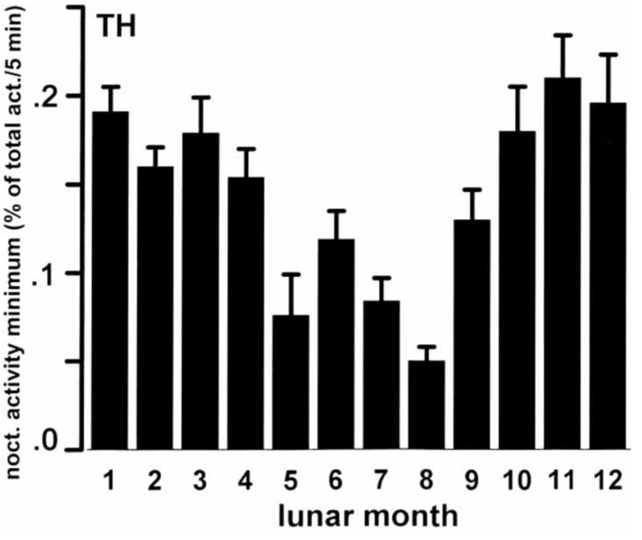

FIGURE 9. Annual variation of the nocturnal minimum of the average (+ SEM) lunar monthly activity patterns. Abscissa: Successive lunar months. Ordinate: Relative activity/5-min bin in % of the lunar monthly average of daily total activity.

In other words, the monkeys tended to terminate their nightly activity period later on warm and on rainy days. A comparison of the phase-angle differences of activity-offset (Figure 4) with precipitation (Figure 1) shows the 3 mo with the largest negative phase-angle differences (i.e., latest activity-offsets) corresponded to the months with highest precipitation. This might have been the main reason for the higher negative correlation of the phase-angle difference of activity-offset with precipitation than with temperature. However, a mono-causal relationship of activity-offset to precipitation can be ruled out, because during lunar mo 1 the relatively large delay of activity-offset still continued despite a pronounced drop in precipitation.

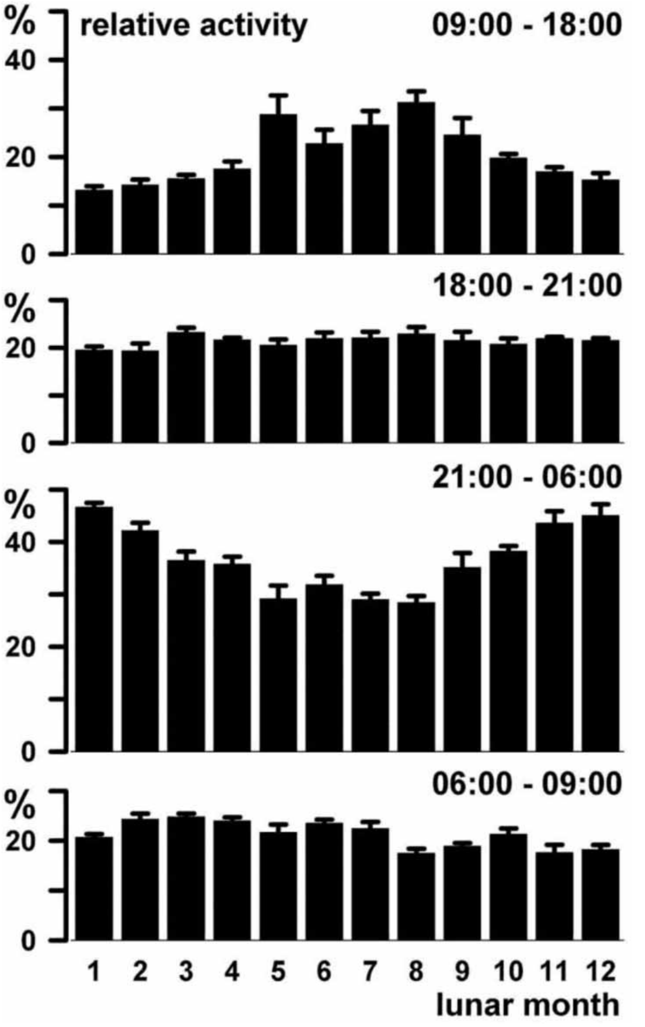

FIGURE 10. Seasonal variation of lunar monthly averages (+ SEM) in the percent proportion of daytime (09:00–18:00 h), dusk (18:00–21:00 h), nighttime (21:00–06:00 h), and dawn (06:00–09:00 h) activity on the respective mean total activity/d.

The phase position of the M peak correlated positively with temperature ($r = .49–.52$, $p < .001$ each), but not with precipitation ($r = .09$, $p = .45$). Average daily amount of activity showed no significant correlation, either with ambient temperature (r = .21–.33, $p = .15–.33$) or with precipitation ($r = .13$, $p = .27$). The same holds for the height of the M peak ($r = –.03$ to $–.204$, $p = .787$ to $.081$). The height of the E peak, as well as the duration of the E and M activity bouts, the nocturnal activity time, and the E peak to M peak interval were negatively correlated with ambient temperature ($p \leq .001$ each). The nightly activity minimum showed a positive relationship with temperature and precipitation ($r = .49–.66$, $p < .001$), whereas the peak-to-peak interval and the duration of the E activity bout were negatively correlated with precipitation ($r = -.45$ and $-.23$, $p < .001$ and $p = .05$, respectively). Hence, both the duration of the evening activity bout and the peak-to-peak interval were shorter on rainy days, whereas the nocturnal activity minimum concomitantly increased, which indicates more body movements and interrupted nightly resting periods on rainy days.

DISCUSSION

Timing of Activity

Under the seasonally changing conditions of the Argentinean Chaco, owl monkeys developed a distinct bimodal nocturnal activity pattern with prominent activity bouts and peaks during dusk and dawn. Both the onset and E activity peak varied in close relationship to sunset. The M activity peak was coupled to sunrise, but the end of the M activity bout was not tightly coupled to it. Thus, no seasonal variation occurred in the phase position of the onset and E peak of activity, whereas the phase position of the M peak and end of activity changed significantly across the year.

The fact that the timing of the daily activity rhythm of owl monkeys varies seasonally in close relationship to sunset and sunrise corresponds to the predictions of the two-oscillator model of circadian rhythmicity (Pittendrigh & Daan, 1976). This model postulates that circadian rhythms are regulated by two endogenous oscillators, an evening oscillator (E) entrained to dusk, and a morning (M) one entrained to dawn. Both oscillators are supposed to be internally coupled so the system usually behaves like one single rhythm (Daan, 2000; Daan & Pittendrigh 1976; Daan et al., 2001; Pittendrigh & Daan, 1976; Schwartz et al., 2001). In support of the two-oscillator hypothesis of circadian rhythmicity, it has recently been shown that in light-entrained mice different subsets of circadianly oscillating SCN neurons may couple to lights-off and lights-on (Ingaki et al., 2007; Naito et al., 2008).

The regulation by a coupled E and M oscillator system enables the daily timing of the E activity bout to change in parallel to sunset, and the M bout to vary with sunrise. In this manner, the owl monkeys' daylight-entrained circadian rhythm adopts a relatively stable phase position of the two main activity bouts to the seasonally varying parameters of the 24-h rhythmicity prevailing in their habitat. The E and M activity peaks correlated better with sunset and sunrise, respectively, than the onset and end of activity did. Therefore, they can be considered better circadian markers in owl monkeys than activity-onset and activity-offset, which, particularly in mammals, mostly serve as behavioral phase markers for the underlying (LD-) entrained circadian rhythm (Daan & Aschoff, 1975). Thus, our data suggest that when studying the timing of mammalian circadian activity rhythms in nature, it may be misleading to only record the overt onset and offset of the daily activity period. Obviously, the timing of the owl monkeys' E activity onset and, in particular, that of the offset of their nocturnal activity time in the morning, are more subject to masking effects of environmental and/or endogenous factors, than the two crepuscular activity peaks. Therefore, the phase positions of the latter correspond better to those of the hypothesized E and M oscillator.

Activity Pattern

Under controlled laboratory conditions, similar prominent E and M activity peaks were less frequently observed in *Aotus lemurinus griseimembra* and *Aotus azarai boliviensis* than in the wild *Aotus azarai azarai*. Pronounced peaks occurred only in a few cases while the circadian activity rhythm free-ran in dim LL, and distinct M peaks were also sometimes observed while the rhythm was entrained by rectangular LD cycles or by skeleton photoperiods (Erkert, 2008; Rappold & Erkert, 1994; Rauth-Widmann et al., 1991, 1996). But only in a few split and internally desynchronized free-running rhythms did two almost equally prominent activity peaks per circadian cycle emerge (Erkert, 2008). Given those findings in closely related taxa, one may conclude that the particular expression of the marked E and M activity bouts in the wild *Aotus azarai azarai* monkeys do not represent a basic characteristic of their circadian activity rhythm, but instead primarily the outcome of masking effects of the diurnally and seasonally varying environmental factors, the most important seeming to be the prevailing luminosity (cf. Erkert, 2008).

During dusk, light intensity first declines from an activity-inhibiting brightness of ≈1000 lux around sunset to a maximally activity-enhancing (or activity-disinhibiting) luminosity of .1 lux, and then to a quite inhibitory low luminance of about 10^{-4} lux at the end of the astronomical twilight (Erkert, 1974, 1976, 2008; Erkert & Groeber, 1986). The reverse happens at dawn. In conclusion, the sunset- and sunrise-related timing of the owl monkeys' E and M activity bouts would mainly result from the light cycle–induced phase setting of the E and M oscillator–regulated E and M activity bouts to certain phases of dusk and dawn. However, their particular shapes and peaks are mainly (co-)determined by strong masking effects of the decreasing and increasing light intensity during dusk and dawn, respectively.

Total Daily Activity

Homeothermic nocturnal mammals from tropical and subtropical environments are expected to show highest total daily activity during the winter months with longest nights. However, the owl monkeys of the Argentinean Chaco developed the least locomotor activity during some of the winter months. This happpened even though the E peak to M peak interval was concurrently the longest. Since this interval is a better marker for the seasonally varying circadian activity time than the entire nocturnal activity time from E onset of activity to M offset of activity, which is more subject to masking, this indicates that the lowest level of nocturnal activity also occurred during these winter months. Accordingly, both the least relative activity between 21:00 and 06:00 h and the lowest nocturnal activity minima were observed in the 8th lunar month (July/August), when nocturnal temperatures were lowest.

The seasonal pattern of the owl monkeys' total daily activity was characterized by a long-lasting main peak from September to December, a smaller peak in March, and lowest activity level in July and August. This pattern cannot be a simple function of the seasonally changing photoperiod and/or of ambient temperature, since both vary in a unimodal manner over the year. On the other hand, precipitation and food availability showed similar seasonal changes with peaks in February/March and October/November, and minimum values from June to August (Fernandez-Duque et al., 2002). As a possible consequence of this pronounced seasonality of food availability, there is in the population a strong seasonal pattern of reproduction, with mating period from April to July and birth season from October to November (Fernandez-Duque, 2009; Fernandez-Duque et al., 2002). Since owl monkeys do not show a conspicuous courtship behavior (Dixson, 1994; Fernandez-Duque et al., 2002), their mating season is not reflected in changes in their activity level. On the other hand, the months with highest activity coincided not only partially with highest precipitation, but also with the birth season (Rotundo et al., 2005) and the energetically most expensive period of lactation and postpartum biparental care. Thus, an increase in the parents' foraging activities, induced by increased energetic demands of pregnancy and biparental care of the offspring, may, at least partly, be responsible for the high activity recorded in November/December.

Although the total daily activity showed no strong relationship with ambient temperature, the relative amounts of nighttime and daytime activity were positively and negatively correlated with it. A study on the thermoregulatory capacity and behavior of owl monkeys, as indicated by the resting metabolic rate at ambient temperatures ranging from 1°C to 39°C, found a rather narrow thermoneutral zone of 28–30°C in an undefined *Aotus* species (Le Maho et al., 1981). At lower temperatures, the monkeys started shivering thermogenesis, and with increasing cold, they adopted a spherical posture to reduce heat loss. With temperatures above 30–33°C, they tried to reduce heat stress by spreading out their extremities and increasing evaporative water loss through panting. Accordingly, wild owl monkeys would be expected to reduce locomotor activity both on very cold and very warm days, the former to save energy and the latter to avoid overheating. These potential thermoregulatory responses may help explain the observed activity minimum during the two coldest months, and the reduced activity level during the two warmest ones.

In conclusion, the seasonal variation of total daily activity in the wild owl monkeys of the Argentinean Chaco results mainly from an interplay of various endogenous and environmental factors. Among these, seasonal changes in ambient temperature, precipitation, and food abundance may play an as important role as masking factors, such as the one played by the annual reproductive cycle and the thermoregulatory and energetical demands and constraints.

Nighttime and Daytime Activity

The bimodal basic activity pattern did not change across the year. Only some of its parameters, such as E and M peak heights, showed some seasonal variation. During the colder short-day half year, the E activity bout lasted longer, and its peak was significantly higher, than during the long-day half year, whereas during the warm long-day months the M activity bout tended to extend and to raise its peak.

Throughout the summer, the nocturnal activity minimum was almost double than during the cold winter half year. This points to a deeper and/or more pronounced nocturnal resting phase during the cold than warm season, and is predicted by the dual-oscillator hypothesis. If during the winter months, the E and M oscillators diverge more from one another due to a larger interval between dusk and dawn to which they are phase-set, then one, indeed, expects a more pronounced gap between the E and M activity bouts. However, given that almost all parameters of the activity pattern were closely related to ambient temperature, this may also be interpreted as evidence of masking by direct temperature effects. That the owl monkeys' circadian activity and body temperature rhythms may, indeed, be strongly masked by ambient temperature has been established in experiments carried out on *Aotus lemurinus griseimembra* (Erkert, 1991). Under constant conditions, the circadian activity and core temperature rhythms of these monkeys free-ran with identical spontaneous periods >24 h. Application of a trapezoidal 24-h temperature rhythm of 20:30°C neither resulted in entrainment nor in distinct relative coordination. However, the still free-running circadian rhythms were markedly modulated; in other words, strongly masked by the 24-h temperature rhythm.

Based on the results of Le Maho et al. (1981), one expects the owl monkeys of the Argentinean Chaco to show more pronounced evening activity bouts throughout the winter months, when relatively milder temperatures in the late afternoon and early night will favor the generation of locomotor activity more than the cold hours of late night and dawn. On the other hand, during the summer months, when relatively high and adverse temperatures occur in the late afternoon and evening, but milder ones during the night and early morning hours, a reverse tendency is expected. Our results are consistent with these predictions. In addition to the temperature-related modifications of the activity pattern, the relative amounts of nighttime and daytime activity also varied seasonally, but in opposite directions.

Nighttime activity was highest during the warm summer months, whereas daytime activity peaked during the cold winter ones. Hence, the seasonal variation from a crepuscular/nocturnal activity pattern during summer to a more crepuscular/cathemeral behavior throughout the winter months seems, at first sight, mainly to result from the masking effects of ambient temperature. However, if one examines the data considering the dual-oscillator model with the assumption that the subjects' central nervous arousal level is driven by an E and M oscillator, one might also expect the owl monkeys to produce more daytime activity during the winter than the summer (cf. Erkert, 2008). However, the fact that the nocturnal activity level, even during winter months, was still higher than the daytime level, argues against such a causal connection. Hence, the hypothesis that the seasonal change from a crepuscular/nocturnal to a more crepuscular/diurnal behavior is a compensatory reaction to the negative masking effects of low temperatures seems the most parsimonious one. The proposition that it results instead from a mechanism towards circadian homeostasis can be ruled out on account of the pronounced annual variation in the daily total activity, which was only about half as high during the winter months than throughout summer.

The lunar periodic and seasonal increase of daytime activity in *Aotus azarai azarai* requires a relatively larger tolerance to higher light intensities. Accordingly, in this owl monkey species, one expects less inhibiting masking effects of bright light on activity than those observed in the more nocturnal *Aotus lemurinus griseimembra* (Erkert, 1974, 1976; Erkert & Groeber, 1986). An additional prerequisite for increased daytime activity in an originally nocturnal species concerns the circadian system itself. Here, a reduction in the amplitude of the underlying circadian oscillation, either by a modification of the circadian clockwork and/or of the involved internal and/or external coupling mechanisms, may also be necessary to enable the circadian timing system to produce considerable amounts of locomotor activity during their circadian resting time, which is phase-set to the bright part of the natural LD cycle. In accordance with that, under controlled laboratory conditions, *Aotus azarai boliviensis* monkeys developed relatively more spontaneous locomotor activity during their circadian resting phase than the more nocturnal and not seasonally cathemeral North Colombian *Aotus lemurinus griseimembra* (Erkert, 2008; Erkert & Cramer, 2006).

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