Daily activity patterns of medium and large neotropical mammals during different seasons in an area of high altitude Atlantic rain forest in the South of Brazil

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Abstract. Camera traps were used to study the daily activity patterns of medium and large mammals (> 1 kg) in an area of Mixed Rain Forest (High Altitude Atlantic Forest) in the South of Brazil. These mammals are adapted to humid forest environments and exhibit seasonal behavior that is different to that of neotropical mammals living in tropical environments. Camera traps without bait were active day and night and through all seasons during the period from March 1999 to December 2010, with a sampling effort of 11,431 trap-days. Species that exhibited diurnal tendencies were *Dasyprocta azarae*, *Eira barbara*, *Nasua nasua* and *Puma yagouaroundi*. The nocturnal species observed were *Dasypus novemcinctus*, *Tamandua tetradactyla* and *Procyon cancrivorus*. *Didelphis aurita*, *Leopardus pardalis* and *L. wiedii* exhibited nocturnal tendencies. *Cerdocyon thous* tended to be more crepuscular than nocturnal. *Puma concolor* exhibited a tendency to nocturnal and crepuscular activity, but diurnal activity was also observed. Finally, the species *Mazama gouazoubira* and *Leopardus tigrinus* were defined as cathemeral. While many species exhibited a tendency for the majority of their activity to be concentrated at certain times, there was no time during which medium and large mammal activity entirely ceased, demonstrating a balanced daily distribution of activity in a Mixed Rain Forest. There were differences in activity patterns between different seasons, especially between summer and winter, with nocturnal species exhibiting a tendency to more intense activity during the first half of the night during the winter and diurnal species tending to be more active at the end of the day during the same season.

Keywords: Araucaria forest, behavior, camera-traps, chronoecology, temporal segregation

Resumo. **Padrão de atividade diária de mamíferos neotropicais de médio e grande porte em diferentes estações do ano em uma área de Floresta Ombrófila Mista no sul do Brasil.** Mamíferos de médio e grande porte (> 1 kg) foram estudados para detecção de padrões de atividade diária em área de Floresta Ombrófila Mista (Floresta Atlântica de altitude) no sul do Brasil. Estes mamíferos adaptados a ambiente de floresta úmida em clima subtropical possuem comportamentos sazonais diferenciados de mamíferos neotropicais vivendo em ambientes tropicais. Armadilhas fotográficas permaneceram em atividade sem utilização de iscas, durante dia e noite ao longo de todas as estações do ano no intervalo entre março de 1999 e dezembro de 2010 com esforço amostral de 11.431 armadilhas-dia. As espécies com tendência diurna foram *Dasyprocta*

azarae, *Eira barbara*, *Nasua nasua* e *Puma yagouaroundi*. As espécies noturnas foram *Dasypus novemcinctus*, *Tamandua tetradactyla* e *Procyon cancrivorus*. As espécies com tendência noturna foram *Didelphis aurita*, *Leopardus pardalis* e *L. wiedii*. *Cerdocyon thous* apresentou tendência mais crepuscular do que noturna. *Puma concolor* mostrou tendência noturna a crepuscular e com ocorrência de atividades diurnas*. As espécies *Mazama gouazoubira* e *Leopardus tigrinus* foram consideradas catemerais. Apesar de as diversas espécies, em sua maioria, apresentarem tendência de concentração de atividade em determinados horários, não houve nenhum horário sem atividade de mamíferos de médio e grande porte, demonstrando equilíbrio de distribuição de atividade ao longo do dia em Floresta Ombrófila Mista. Houve diferenças nos padrões de atividade entre diferentes estações, especialmente entre verão e inverno, com espécies noturnas mostrando tendência a maior atividade durante a primeira metade da noite durante o inverno, enquanto espécies diurnas tenderam a ser mais ativas no final do dia durante esta estação.

Palavras-chave: Floresta com araucárias, comportamento, armadilhas fotográficas, cronoecologia, , segregação temporal.

INTRODUCTION

Temporal ecological niches are determined by the daily cycle of solar illumination (daytime) and darkness (nighttime) which, modulated by moonlight, serves as a reference point, since these are periodical and predictable changes to which animals' endogenous rhythms are synchronized (Morgan, 2004). The relationship between the time a given individual spends in activity and the time it spends at rest is one of the most important characteristics it shares with other members of its own species (Marques, 2004). A species will only develop a pattern of activity in the presence of conditioning factors that stimulate active or resting behavior, and this behavioral pattern is modulated by the brightness of light in the surrounding environment (Erkert *et al.,* 1976). In nocturnal animals the circadian pacemaker takes twilight as its primary signal, adjusting the start of their activities to the beginning of the night throughout the year, keeping their endogenous rhythm synchronized with the 24-hour-per-day external rhythm (Schwitzer *et al.,* 2007). Electrical cauterization of the suprachiasmatic nucleus of small diurnal rodents caused them to become nocturnally active as well, leading to higher predation rates due to the nonadaptive behavior (Decoursey, 2004). Physiological parameters such as body temperature, enzyme activity, photoreceptor sensitivity, and storage or tapping of energy resources all need to adjust to expected environmental changes before they occur (Kronfeld-Schor & Dayan, 2003). To correctly understand animals' adaptations to environmental changes, it is necessary to consider both internal biological rhythms and interactions between the organism and its environment (Marques, 2004). In view of the

importance of the effects that light intensity has on physiology and behavior, twilight hours must be taken into consideration when recording the activity of animals in the wild.

Animals' adaptations to periodic environmental changes involve anatomic, physiological and behavioral changes. Behavior is a variable phenotype resulting from interaction between environmental changes and the animal's internal state, of which its endogenous pacemaker is a part (MORGAN, 2004). Circadian rhythms allow animals to anticipate environmental changes, making use of the best time of day for certain activities, and the mechanism that determine these rhythms can affect the plasticity of their responses to selective ecological forces (KRONFELD-SCHOR & DAYAN, 2003). By changing their activity patterns between periods with high or low intensity light, animals are able to choose between geographically identical habitats that differ in terms of geophysical and biological characteristics (MORGAN, 2004). Furthermore, if animals' endogenous temporal mechanisms are to be understood, it is necessary to consider their interactions with other activities of adaptation to their environments, such as seeking sexual partners and relationships involving predation, parasitism and competition for limited resources (MARQUES, 2004).

Daily activity patterns can be subdivided into the following chrono-ecotypes: diurnal, nocturnal, crepuscular and cathemeral (active behavior occurs equally at night and during the day). Mammalian chrono-ecotypes are not rigid

systems that are constricted to a single temporal niche, but can vary depending on need as determined by environmental conditions (ERKERT, 2008). Diurnal and nocturnal ways of life involve complex adaptations and what is a beneficial adaptation in one activity pattern can be harmful in another (KRONFELD-SCHOR & DAYAN, 2003).

Regions at higher latitudes exhibit drastic changes in photoperiod, which influences the activity of animals. Activity times tend to change in accordance with the seasonal changes in the length of the day for diurnal species or of the night for nocturnal species, but mammals exhibit less extreme reactions to the photoperiod than do birds (DAAN & ASCHOFF, 1975). The climate affects the abundance and quality of vegetation used as food sources and adverse climatic conditions increase the risk to animals of hyperthermia or hypothermia (BOURGOIN et al., 2008). The combination of seasonal variations in photoperiod and in other environmental conditions such as temperature and availability of food can provoke activity patterns that are different from those that would result from mere variations in the length of the day (PITA et al., 2011). Animals engage in seasonal movement as one means of achieving thermoregulation and of obtaining food resources and access to partners for reproduction (LONG et al., 2013). In general, studies of the ecology of mammals in the wild fail to take the physiological basis of their behavior into account, but this cannot be ignored.

Studying the activity patterns of animals in the wild creates new scientific knowledge

(behavioral, ecological), but it can also have practical uses, such as documenting changes caused by fragmentation of habitats (NORRIS *et al.,* 2010), investigating changes in animals' behavior in response to human persecution (KITCHEN *et al.,* 2000), and understanding patterns of wild animal deaths caused by human transportation (ANDO, 2003); in short, it has many applications within conservation biology.

In academic terms, the tendency has been to investigate daily activity patterns of neotropical mammals in the wild in conjunction with other features of their biology and ecology, with no specific objective of discussing the temporal aspects of their behavior (LOUGHRY & MCDONOUGH, 1998; MAFFEI *et al.,* 2005; CUELLAR *et al.,* 2006; MAFFEI *et al.,* 2007; GALLIEZ *et al.,* 2009; FARIA-CORRÊA *et al.,* 2009; VANDERHOFF *et al.,* 2011; MONROY-VILCHIS *et al.,* 2011; SALVADOR & ESPINOSA, 2015; BLAKE *et al.,* 2016; TORRE *et al.,* 2016; FERREGUETTI *et al.,* 2018). In general, those studies that have been conducted specifically into daily activity patterns have been restricted to one or a few species *Didelphis albiventris* (OLIVEIRA-SANTOS *et al.,* 2008); *Dasypus novemcinctus* (MCDONOUGH & LOUGHRY, 1997; ANCONA & LOUGHRY, 2009); *Dasyprocta punctata* (LAMBERT *et al.,* 2009); *Didelphis marsupialis, Dasypus novemcinctus* and *Dasyprocta leporina* (NORRIS *et al.,* 2010); *Cuniculus paca* (MICHALSKI & NORRIS, 2011); *Tapirus terrestris* (OLIVEIRA-SANTOS *et al.,* 2010); *Leopardus pardalis* and its potential prey (PORFIRIO *et al.,* 2016 a); *Panthera onca* and *Puma concolor* and their prey

(PORFIRIO *et al.,* 2016 b). Studies of mammalian assemblages have revealed coexistence of diurnal, nocturnal, crepuscular and cathemeral species in a number of different forest environments such as semideciduous seasonal forest in a subtropical climate (KASPER *et al.,* 2007), an area of transition between Amazonian forest, Cerrado savannah and secondary forest (NEGRÕES *et al.,* 2011), Amazonian pre-Andean seasonal forest at altitudes from 1000 to 1200 m (GÓMEZ *et al.,* 2005) and in montane cloud forest (JIMÉNEZ *et al.,* 2010). An investigation of several neotropical species can be found (GÓMEZ *et al.,* 2005), but that study did not conduct quantification that would make it possible to compare the results with other assemblages living in different environments. The majority of studies of neotropical mammalian species have been conducted in tropical environments, where differences between seasons in terms of day-night duration and temperature are not significant factors.

The species richness of mammals in the region where this study was conducted (the Araucaria High Plains in the South of Brazil) is at least 66 native wild species and one exotic species, 30 of which are medium-size or large (MARQUES *et al.,* 2011). The objectives of this long-term study were to quantify the activity patterns of medium and large mammals in a Mixed Rain Forest or Araucaria Forest (Atlantic Rain Forest with a subtropical climate) where there are seasonal differences in temperature and food availability. Our hypotheses are as

follows: 1. this assemblage of mammals has a very balanced daily temporal distribution, without any periods in which there is no activity; 2. there are significant seasonal differences in times of activity, with particular emphasis on winter, when temperatures are lower, especially, at night.

Materials and Methods

Study area

Fieldwork was conducted in the "Araucaria High Plains" in the São Francisco de Paula National Forest (FLONASFP), Rio Grande do Sul, in South Brazil at geographical coordinates 29°23'S and 50°23'W. It is a sustainable use conservation unit, with an area of 1,606.7 ha, a mean altitude of 930 m and vegetation forming a natural mosaic comprising mixed rain forest (901.9 ha), native pine plantations (*Araucaria angustifolia*) and silviculture of the exotic species *Pinus* sp. and *Eucalyptus* sp. Additionally, supplementary data were also collected within the Pró-Mata Nature Research and Conservation Center (CPCN Pró-Mata), a privately-owned protected area of 4,500 ha at geographical coordinates 29°28'S and 50°10'W, at altitudes varying from 600 to 900 m, with vegetation associated with Atlantic rain forest (mixed rain forest, dense rain forest in the foothills, grasslands). The region has a Cfb humid subtropical climate according to the Köppen-Geiger general system. Mean annual precipitation is 2,240 mm, there is no dry season, temperatures observed for the coldest month of the year (winter) range from -6.5°C to 28°C and during the hottest month (summer) temperatures range from 4.5°C to 34°C (Cademartori *et al.,* 2002). Between 2002 and 2009 temperatures recorded at the FLONASFP head office ranged from an absolute minimum of -3° C in the winter to an absolute maximum of 34.5° C in the summer (personal communication, Edenice Brandão Ávila de Souza, 2011).

Data collection in the field

Camera traps equipped with active sensors (Marques & Ramos, 2001) and analogue cameras with a time-stamp function were used to record the activities of medium and large mammals with body mass greater than 1 kg (Chiarello, 2000). The camera-traps were placed along unpaved roads between plantation stands or along animal trails within the forest. No bait was used and the distance between sampling stations was 500 m. Sampling effort was 11,431 trap-days from March 1999 to December 2010 within the FLONASFP (10 camera traps set in pairs on either side of a track) and 78 trap-days between February 1999 and September 2002 in a sporadic manner within the CPCN Pró-Mata (13 three-day expeditions using two camera traps placed separately). Camera traps were operational 24 hours per day [active sensors can be used during daylight and in the daytime heat because they are not dependent on heat radiated by the animals' bodies (Marques & Mazim, 2005)] and sampling was conducted during all seasons of the year (during the autumn and winter months, when the temperatures are lower, batteries in equipment were replaced with

greater frequency to guarantee it would continue working in the more adverse conditions). Thus, daytime and nighttime hours and all four seasons were sampled in equilibrium. If the same species was recorded more than once in succession at the same place with an interval of less than one hour, then only one record was considered valid, in order to preserve independence of samples.

DEFINITIONS OF SEASONS OF THE YEAR AND PERIODS OF THE DAY

Data on daily photoperiods for the area (Southern hemisphere) were obtained from the Brazilian national observatory. At the latitude of the study site, the shortest days have a photoperiod of 10h15min in June (winter) and the longest days last 14h02min and are in December (summer). The seasons were delimited by the solstices (21st June in winter and 21st December in summer) and equinoxes (20th March in autumn and 23rd September in spring) (OBSERVATÓRIO NACIONAL, 2011). The exact times of twilight in the morning (dawn) and evening (dusk) were used to mark sunrise and sunset with precision. The periods from one hour before to one hour after these exact times were defined as twilight (THEUERKAUF et al., 2003), so that each day had four twilight hours (two hours each either side of sunrise and sunset), irrespective of season. As such, the only period with a fixed number of hours all year long was twilight, while diurnal and nocturnal periods lasts for differing durations depending on the natural photoperiod of the different seasons of the year.

Starting at the exact time of sunset, independent photo-capture events were grouped by one-hour intervals, until the next nightfall (the time of each photograph was recorded on it). This resulted in photo-capture frequencies for each species by one-hour intervals starting at sunset. The time that the twilight hours fell throughout the year as the seasons changed was therefore tied to the phenomenon of the sunlight intensity gradually dimming as night falls, irrespective of the length of the photoperiod. This method of demarcation that takes the time of sunset into account is designed to remove the arbitrary element that would be introduced by using fixed times on the clock, since the most important signal for synchronization of animals' endogenous rhythms is the quantity of ambient light and not the time of day itself.

CLASSIFICATION OF CHRONO-ECOTYPES

Independent photographic records were classified and quantified according to activity periods defined by JIMÉNEZ et al., 2010 as follows: diurnal species (less than 10% of records during dark periods), nocturnal species (more than 90% of records during dark periods), species with a diurnal tendency (between 10 and 30% of records during dark periods), species with a nocturnal tendency (from 70 to 90% of records during dark periods), crepuscular species (at least, 50% of observations during crepuscular periods) and cathemeral species (activities well distributed between light and dark periods).

STATISTICAL ANALYSES

Data were analyzed on Oriana versions 3 (KOVACH, 2009) and 4 software (KOVACH, 2011) for circular statistics using the Rayleigh test of uniformity and Rao's spacing test, with the objective of examining data that are distributed in a circular manner, such as time (LEHNER, 1996).

Circular statistical analyses were conducted for 14 species for which there was a minimum of 12 photo-captures, with the objective of determining mean vectors of hours in activity and the circular standard deviation and variance and their respective 95% confidence intervals. The mean vector has two properties: mean angle (µ) and length (r). The first is expressed as the time of day, or angle, that represents the mean time of each species' activities. The second property can vary from 0 to 1, with higher values indicating that observations are grouped around the mean, while smaller values indicate that observations are not concentrated.

The Rayleigh test of uniformity (Z) was used to determine whether sample times were significantly different from what would be expected by chance. Higher values of Z indicate greater concentration of the data around the mean (lower probability that data are uniformly distributed). Probabilities below the significance level of 0.05 indicate that data are not distributed uniformly and are evidence of a trend. Rao's spacing test (U) tests spacing between adjacent points around a circle. Small p values mean that spacing is not uniform.

The Mardia-Watson-Wheeler test (ZAR, 2010) was used to investigate whether there were significant differences in time of activity between the four seasons and for all 14 species together, for the group of four diurnal species, for the group of seven nocturnal species and separately for the seven species that were recorded in at least 18 photo-captures in each of the four seasons. This statistical method is appropriate for circular, continuous and nonparametric data and analyses are possible with a minimum of 17 samples. This stricture was respected in analyses of separate species for each of the four seasons. The diurnal species and the nocturnal species were each grouped together and considered as temporally distinct assemblages. An assemblage was defined as a group of phylogenetically related species that share a common resource and occur in the same community (FAUTH et al., 1996). In this case, temporally similar species share periods of time (the nocturnal species, which take sunset as their most important signal for the start of activity, and the diurnal species, whose signal to start activity is sunrise).

Data for the species *Mazama gouazoubira* were broken down and analyzed separately for adults (individuals with or without horns but without lateral spots on the body) and juveniles (individuals without horns and with lighter spots on the body) which may or may not be photographed when accompanied by adult females. Juveniles sometimes jump along in front of the adult females (personal observation) and if they are caught on camera and then come back

and take a different direction, the adult females are not captured. Adult females that were captured with juveniles were not included with the data for adult individuals, but were considered to be with the juveniles and, therefore, to potentially exhibit different behavior to solitary adults.

The Kruskal-Wallis test (ZAR, 2010) was employed to verify whether there were differences in activity over the 24 hours period for the medium and large animal assemblage as a whole.

RESULTS

The sampling effort expended in the FLONASFP returned 1,386 independent photo-captures with full time and date records for 14 species of medium and large mammals. The number of records of *Cerdocyon thous* (crab-eating fox) from the FLONASFP was supplemented with eight independent photo-captures of the species within the CPCN Pró-Mata. For each species, photo-captures were classified by period of day (D = diurnal, C = crepuscular and N = nocturnal) (Table 1) and circular statistics were calculated (Table 2).

Different species exhibited propensities to specific activity patterns (Figure 1). Species with a diurnal tendency were as follows: *Dasyprocta azarae*, *Eira barbara*, *Nasua nasua* and *Puma yagouaroundi*. The nocturnal species

Table 1. Number of photo-captures recorded in an area of mixed rain forest (part of the Atlantic rain forest) from March 1999 to December 2010, by period of day.

Species	Captures	D(%)	C(%)	N(%)
Didelphis aurita (Wied-Neuwied, 1826) black-eared opossum	141	1 (0.72%)	20 (14.18%)	120 (85.1%)
Dasypus novemcinctus Linnaeus, 1758 nine-banded armadillo	153	4 (2.61%)	10 (6.64%)	139 (90.85%)
Tamandua tetradactyla (Linnaeus, 1758) lesser anteater	12	0	0	12 (100%)
*Dasyprocta azarae (*Lichtenstein, 1823) Azara's agouti	256	152 (59.38%)	97 (37.89%)	7 (2.73%)
Mazama gouazoubira (G. Fischer, 1814) gray brocket deer	123	50 (40.65%)	22 (17.89%)	51 (41.46%)
Eira barbara (Linnaeus, 1758) tayra	55	46 (83.64%)	6 (10.91%)	3 (5.45%)

Table 1. Continuation.

Nasua nasua (Linnaeus, 1766) South American coati	59	51 (86.44%)	8 (13.56%)	0
Procyon cancrivorus (G. Cuvier, 1798) crab-eating raccoon	140	1 (0.71%)	10 (7.15%)	129 (92.14%)
Cerdocyon thous (Linnaeus, 1766)* crab-eating fox	23	1 (4.35%)	10 (43.48%)	12 (52.17%)
Leopardus wiedii (Schinz, 1821) margay cat	27	3 (11.11%)	5 (18.52%)	19 (70.37%)
Leopardus tigrinus (Schreber, 1775)** little spotted cat	158	49 (31.01%)	44 (27.85%)	65 (41.14%)
Leopardus pardalis (Linnaeus, 1758) ocelot	181	20 (11.05%)	24 (13.26%)	137 (75.69%)
Puma concolor (Linnaeus, 1771) puma or cougar	40	5 (12.5%)	15 (37.5%)	20 (50%)
Puma yagouaroundi (E. Geoffroy Saint-Hilaire, 1803) jaguarondi	27	22 (81.48%)	4 (14.82%)	1 (3.7%)

D: diurnal; C: crepuscular; N: nocturnal

*Eight photo-captures in the CPCN Pró-Mata, all others in the FLONASFP

(Scientific names of mammals according to Wilson & Reeder (2005)

Table 2. Results of circular statistical analysis of times of activity of 14 species of mammal (> 1 kg) in mixed rain forest in São Francisco de Paula, RS, Brazil.

Species	r	Mean Vector	Circular Variance	Circular standard deviation	95 % Confid. Interval	Z	U (µ)
D. aurita	0.700	22:57	0.300	03:13	22:25 23:29	69.162 p<1E-12	207.133 p < 0.01
D. novemcinctus	0.709	23:41	0.291	03:09	23:11 00:11	76.992 p<1E-12	204.485 p < 0.01

Table 2. Continuation.

T. tetradactyla	0.754	01:46	0.246	02:52	23:55 03:36	6.819 p=3.80E-4	209.75 p < 0.01
D. azarae	0.473	14:05	0.527	04:40	13:26 14:45	57.212 p<1E-12	195.344 p < 0.01
M. gouazoubira	0.012	03:26	0.988	11:18	-	0.019 p= 0.981	124.585 0.9>p>0.5
E. barbara	0.697	12:57	0.303	03:14	12:06 13:49	26.694 p=2.55E-12	193.341 p < 0.01
N. nasua	0.668	12:29	0.332	03:25	11:36 13:22	26.333 p=3.66E-12	214.483 p < 0.01
P. cancrivorus	0.678	23:39	0.322	03:22	23:05 00:13	64.352 p < 1E-12	194.714 p < 0.01
C. thous	0.422	00:58	0.578	05:01	-	4.089 p = 0.015	184.891 p < 0.01
L. wiedii	0.476	23:41	0.524	04:39	21:40 01:41	6.128 p=0.002	157.417 0.1>p> 0.05
L. tigrinus	0.148	05:19	0.852	07:27	-	3.468 p = 0.031	134.462 0.5 > p > 0.1
L. pardalis	0.466	00:21	0.534	04:43	23:33 01:09	39.315 p < 1E-1	162.814 p < 0.01
P. concolor	0.350	00:32	0.650	05:31	22:13 02:51	4.907 p = 0.007	147 0.5 > p > 0.1
P. yagouaroundi	0.596	11:43	0.404	03:53	10:12 13:15	9.592 p= 2.91E-5	196.083 p < 0.01

(-) not calculated because of low concentration of data; Rayleigh test of uniformity (Z) and Rao's spacing test (U)
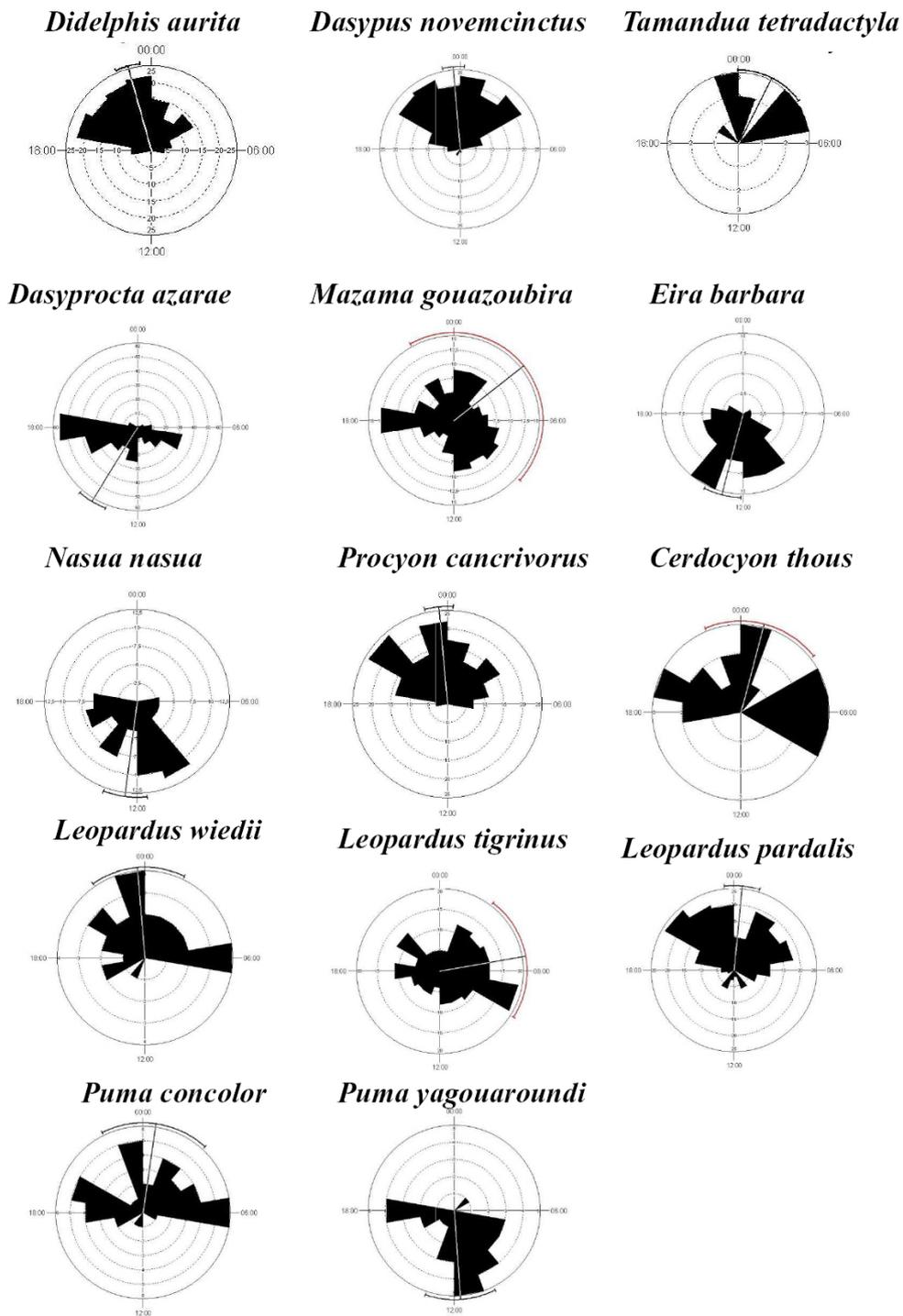
Figure 1. Activity patterns of 14 species of medium and large mammals in mixed rain forest in São Francisco de Paula, RS, Brazil. The numbers around the edges of circles indicate time of day (06h on the right; 12h at the bottom; 18h on the left; 00h at the top); the radius indicates the mean vector; the curved line represents the confidence interval for the mean.

were: *Dasypus novemcinctus*, *Tamandua tetradactyla* and *Procyon cancrivorus*. The species with a nocturnal tendency were: *Didelphis aurita*, *Leopardus pardalis* and *L. wiedii*. A more crepuscular than nocturnal tendency was observed for *Cerdocyon thous*. *Puma concolor* exhibited nocturnal and crepuscular tendencies, but was also active during the day. *Mazama gouazoubira* and *Leopardus tigrinus* were defined as cathemeral, because they did not exhibit any definite tendency, with activities evenly distributed across all periods.

According to measures of both uniformity and spacing, the majority of species (71.43%) had activity concentrated in certain periods (p < 0.05). *Mazama gouazoubira* and *Leopardus tigrinus* did not exhibit a tendency to activity in any specific period, with times of records of activity uniformly distributed across 24 hours (Table 2).

Analysis of the hours during which the 14 species tended to be active were analyzed for each season separately, showing that summer and spring were not significantly different.

However, all other possible combinations of two seasons were different from each other (Table 3). The four diurnal species did not exhibit significant differences in activity between the four seasons, but the seven nocturnal species only failed to exhibit differences for the combinations summer versus spring and winter versus autumn (Table 3).

Among the seven species with the largest numbers of captures for all seasons, there were no significant differences in activity times for *Didelphis aurita*, *Mazama gouazoubira*, *Leopardus tigrinus* or *L. pardalis*. *Dasypus novemcinctus* only exhibited a difference between winter and spring. *Dasyprocta azarae* exhibited significant differences between winter and each of the other three seasons, which were not different from each other. *Procyon cancrivorus* exhibited the greatest number of differences in times of activity between different seasons, with summer different from autumn, summer different from winter and autumn different from spring (Table 4).

Table 3. Results of the Mardia-Watson-Wheeler test comparing hours of activity of paired samples of seasons for nocturnal and diurnal species separately occurring in the São Francisco de Paula National Forest.

Groups of Species	Sum X Aunt	Sum X Win	Sum X Spr	Aunt X Win	Aut X Spr	Win X Spr
7 nocturnal species	W = 8.41 p = 0.0015*	W = 9.274 p = 0.01*	W = 0.456 p = 0.804	W = 3.04 p = 0.219	W = 8.307 p = 0.016*	W = 11.241 p = 0.004*
4 diurnal species	W = 0.189 p = 0.91	W = 5.921 p = 0.052	W = 0.793 p = 0.673	W = 4.046 p = 0.132	W = 0.445 p = 0.801	W = 3.837 p = 0.147

W = Mardia-Watson-Wheeler test   * (p < 0.05)
Sum = summer; Aut = autumn; Win = winter; Spr = spring

Table 4. Results of the Mardia-Watson-Wheeler test comparing hours of activity of paired samples of seasons for seven species of medium and large mammals occurring in the São Francisco de Paula National Forest, RS, Brazil.

Species	Sum X Aunt	Sum X Win	Sum X Spr	Aunt X Win	Aut X Spr	Win X Spr
Didelphis aurita	W=2.006 p=0.367	W=3.548 p=0.17	W=1.326 p=0.515	W=1.878 p=0.391	W=0.171 p=0.918	W=2.477 p=0.29
		(N: Sum = 18	Aut = 22	Win = 68	Spr = 33)	
Dasypus novemcinctus	W=2.638 p=0.267	W=2.1 p=0.35	W=2.932 p=0.231	W=2.497 p=0.287	W=4.229 p=0.121	W=10.305 p=0.006*
		(N: Sum = 59	Aut = 23	Win = 18	Spr = 53)	
Dasyprocta azarae	W=0.348 p=0.84	W=9.271 p=0.01*	W=0.51 p=0.775	W=11.1 p=0.004*	W=2.243 p=0.326	W=10.195 p=0.006*
		(N: Sum = 40	Aut = 65	Win = 78	Spr = 73)	
Mazama gouazoubira	W=1.156 p=0.561	W=2.683 p=0.261	W=0.824 p=0.662	W=0.716 p=0.699	W=0.43 p=0.806	W=1.188 p=0.552
		(N: Sum = 25	Aut = 26	Win = 45	Spr = 27)	
Procyon cancrivorus	W=7.181 p=0.028*	W=6.453 p=0.04*	W=0.432 p=0.806	W=1.545 p=0.462	W=7.17 p=0.028*	W=4.955 p=0.084
		(N: Sum = 28	Aut = 35	Win = 36	Spr = 40)	
Leopardus tigrinus	W=1.528 p=0.466	W=4.141 p=0.126	W=2.714 p=0.257	W=2.144 p=0.342	W=1.899 p=0.387	W=4.83 p=0.089
		(N: Sum = 21	Aut = 44	Win = 73	Spr = 18)	
Leopardus pardalis	W=0.033 p=0.984	W=0.293 p=0.904	W=0.492 p=0.782	W=0.43 p=0.807	W=0.402 p=0.818	W=1.329 p=0.514
		(N: Sum = 39	Aut = 32	Win = 67	Spr = 43)	

W = Mardia-Watson-Wheeler test   * (p < 0.05)

Sum = summer; Aut = autumn; Win = winter; Spr = spring

Adult *Mazama gouazoubira* exhibited a distinct time of activity to juveniles (which may or may not have been accompanied by an adult female). Whereas mean time of activity for juveniles was at 11h09min and their 95% confidence interval was from 09h24min to 12h55min, with a diurnal activity pattern (Figure 2), the adults' mean time of activity was 23h39min,
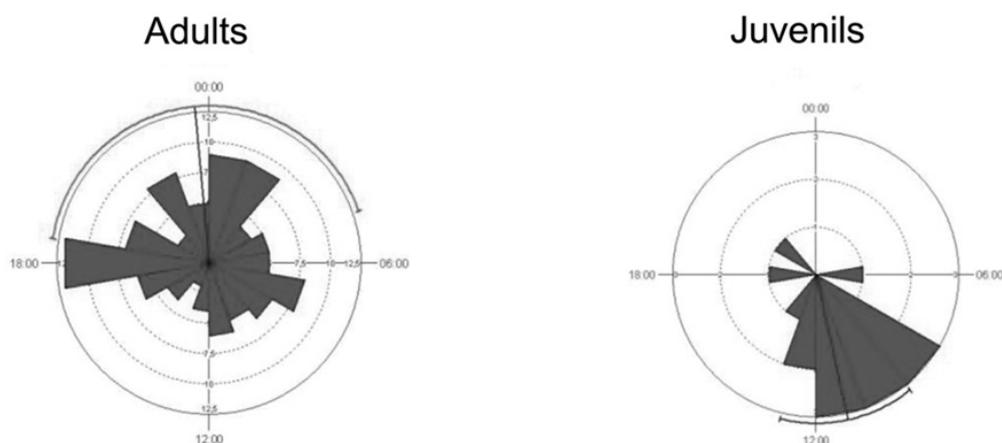
Adults

Juvenils

Figure 2. Activity patterns of adult and juvenile *Mazama gouazoubira* (gray brocket deer) in mixed rain forest in São Francisco de Paula, RS, Brazil (The length of the curved line for adults indicates a low concentration of data) adults n = 110 juvenils n = 13.

although calculation of their confidence interval was invalidated by the uniformity of data distribution or by low concentration of data.

By grouping photo-capture events into one-hour intervals timed from sunset, activity patterns were organized into categories based on the gradual dimming of sunlight at the end of the day, irrespective of the season and variations in photoperiod (Figure 3). Taking all 14 species together, activity was uniformly distributed across all of the one-hour periods timed from sunset onwards (Figure 3), (H = 16.96   Hc =
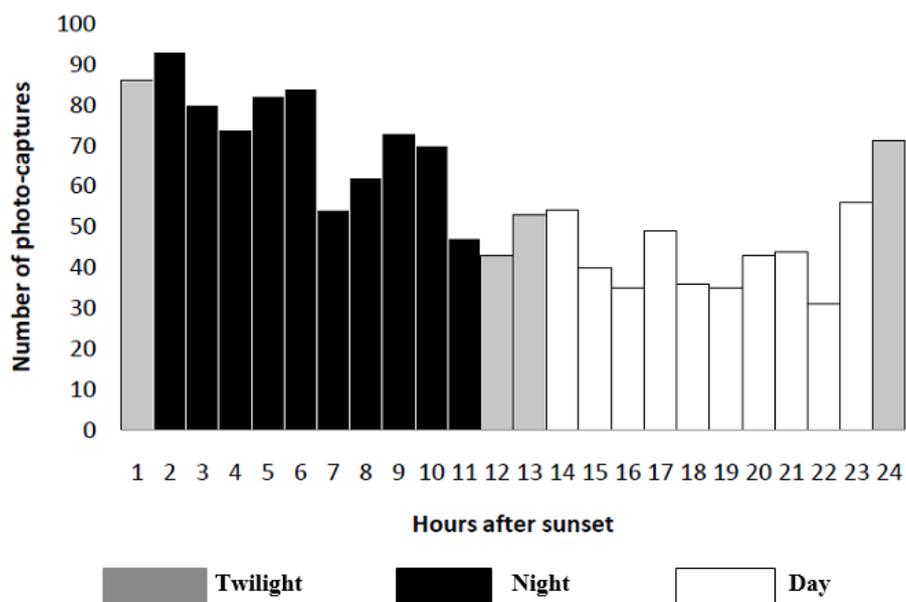

Figure 3. Frequencies of photo-captures of 14 species of medium and large mammals, by one-hour intervals starting at sunset.

17.66 p = 0.7758), indicating that at all times of day some medium to large mammal or another was active, with no times at which activity was significantly reduced.

Discussion

Although the majority of species recorded had nocturnal or predominantly nocturnal activity, the daily temporal distribution of the medium and large mammal assemblage was distributed across all of the one-hour intervals timed from sunset. This was the result of the eminently diurnal pattern of certain species, which was most conspicuous in *Dasyprocta azarae*, with a high frequency of photo-captures.

Differences observed between different seasons, especially between summer and winter, revealed that, in general, the nocturnal species tended to utilize the first half of the night most intensely during winter, whereas the diurnal species tended to use the end of the day more during winter. The behavior of the nocturnal species may reflect a quest for thermal comfort during the earlier hours of the night when the ambient temperature has not yet reached its lowest point. The activity of the diurnal species probably intensifies at the end of the day as they search for food that they have not yet found during the shorter winter days.

Didelphis aurita exhibited higher peaks of activity during the first half of the night and photoperiod has an influence on the start of its activity. The later the sun sets, the later at night their records begin. This pattern of activity

starting close to sunset is also observed in other neotropical marsupials. In a region of Amazonian forest, *Didelphis marsupialis* had mean activity at 22h52min (95% CI = 22h05min to 23h40min) with a range from 16h57min to 06h04min (Norris *et al.,* 2010), which is not very different from the results observed in mixed rain forest. *Didelphis albiventris* (white-eared opossum) has terrestrial and scansorial habits and its temporal pattern has an activity peak soon after sunset, with activity reducing later during the night (Oliveira-Santos *et al.,* 2008). The same authors observed a similar pattern for *Micoureus paraguayanus* with arboreal habits. These studies were conducted using methods that did not imprison the animals in traps, avoiding the methodological bias by which activity would apparently be greater at the start of the night because captured animals remain trapped and are unable to continue their normal activity (Hicks *et al.,* 1998; Castro-Arellano & Lacher Jr., 2009; Larrucea & Brussard, 2009). Using bait, as is done in some studies, could change some animals' behavior, but the fact that animals are not trapped in cages allows them to continue their activities for the remainder of the night. In North America, neither sex nor age classes had an influence on the activity pattern of *D. virginianus*, and mean capture time was 22h43min, with two capture events during the daytime (Carver *et al.,* 2011). More intense activity at the start of the night was also observed for *Chironectes minimus*, which has aquatic habits (Galliez *et al.,* 2009). The females of this species were more active than the males during the first period of the night,

while the males were more active during the dry season (which coincides with their reproductive period), probably in search of females (Leite *et al.*, 2013). Despite differences in ecology and habitat between these species, their behavior in response to the gradual reduction in light is similar. Periods of activity observed for many different species of medium-sized didelphimorph did not diverge notably in different types of climate or environment or on the basis of similar or different habits. This adds weight to the idea of phylogenetic inertia with respect to the activity patterns of neotropical marsupials (Leite *et al.,* 2013).

Procyon cancrivorus also exhibits a nocturnal activity pattern in other types of forest in South America (Gómez et al., 2005; Kasper et al., 2007; Arispe *et al.*, 2008). In the United States, *Procyon lotor* exhibits a strongly nocturnal activity pattern, between sunset and dawn, with a mean capture time of 22h20min (Carver *et al.,* 2011). In the southern hemisphere, *Procyon cancrivorus* and *Didelphis aurita* exhibited the same overlap of periods of activity observed by Carver *et al.,* 2011 for *Procyon lotor* and *Didelphis virginiana* in the Northern hemisphere. The pattern of activity of *Procyon cancrivorus* was significantly different for summer versus winter, summer versus autumn and autumn versus spring, as a consequence of the changes in times of greatest numbers of photo-captures, from the first half of the night during the winter, through dispersed distribution of activity throughout the night and less concentrated activity during the middle

of the night in autumn and then a tendency to concentrate activity in the middle of the night in spring, until the arrival of summer, when there is the greatest concentration of activity in the middle of the night. The greater concentration of activity during the first half of the night in winter may be related to reducing the level of thermal stress caused by low temperatures, especially during the winter nights. At the start of the night, temperatures have not yet fallen to their lowest point and there is relative thermal comfort for these animals. Changes in activity patterns that avoid thermal discomfort are observed in many different species of mammals living in very different environments and climates (Georgii & Schröder, 1983; Bourgoin *et al*., 2008; Vieira et al., 2010; Pita et al., 2011).

The mean activity time of *Dasypus novemcinctus* (23h41min) was not greatly different from records for the same species in an area of Amazonian forest, where mean activity was at 22h20min (95% CI = 21h39min to 23h02min) with a range of 17h40min to 15h56min (Norris *et al.,* 2010). According to these authors, the size of forest fragments impacted on activity times, with activity starting later in large areas (more than 1000 ha of forest) with no occurrence of diurnal activity, whereas in smaller areas diurnal activity was more intense. In Belize, this species exhibited 96.4% nocturnal and 3.6% crepuscular activity (Weckel *et al.,* 2006). In Florida, United States (30°N), this species did exhibit diurnal activity, especially among young individuals, but the majority of animals exhibited nocturnal

activity with peak activity at the start of the night soon after sunset (McDonough & Loughry, 1997). In the present study (30°S), this species tended to become active one hour after sunset, with activity becoming more intense up to two hours after nightfall and possibly extending throughout the night until dawn. There was a significant difference between activity during the winter and the spring, since this species was active less frequently in winter, with activity concentrated in the first half of the night, whereas it was more active during spring and activity was recorded throughout the whole night without interruptions. The thermoregulatory capacity of *Dasypus novemcinctus* is considered primitive because of the relative oscillation of these animals' body temperature (McBee & Baker, 1982). In Florida, armadillos began activity before sunset, while activity began up to 2 hours after sunset in Atlantic rain forest in the southeast of Brazil, with young individuals active during the summer (Loughry & McDonough, 1998). The pattern observed in the present study in Mixed Rain Forest in the South of Brazil is more similar to what occurs in Atlantic Rain Forest in the Southeast of Brazil than to what has been observed in the Northern hemisphere. These animals are active for a period of four to six hours per day and rest in their burrows for around 20 hours per day, with displacements of less than 200 m between successive locations (Ancona & Loughry, 2009). The finding reported by Norris *et al.,* 2010 that nine-banded armadillos respond to the degree of habitat fragmentation by changing their activity patterns raises the possibility that the records of diurnal activity in the present study could be related to the fact that the mixed rain forest (901.9 ha) within the conservation unit studied is only a fragment of what was originally the south Brazilian Atlantic rain forest (SOS Mata Atlântica & INPE, 2010). Notwithstanding, the only records of daytime activity of nine-banded armadillos within the FLONASFP were made during summer and it is possible that these were young individuals.

Plasticity of time of activity allows *Mazama gouazoubira* populations to adapt to the conditions in the environment where they live. This cervid is believed to be able to occupy degraded areas, as long as there are remnants of forest or savannah vegetation to provide shelter during daylight hours (Duarte, 1996). This species has also exhibited activity at different times in different types of environment (Rivero et al., 2005; Negrões et al., 2011). There are three basic forms of cathemeral activity: seasonal alternation between predominantly diurnal and predominantly nocturnal activity; seasonal alternation from a diurnal pattern to activity throughout the 24 hours; and activity throughout the 24 hours all year long (Tattersall, 2006). In the FLONASFP, the activity patterns of *Mazama gouazoubira* did not exhibit seasonal differences and so it is classified in the third basic type of cathemerality. In the Pantanal, *Mazama gouazoubira* exhibited a similar activity pattern to *Puma concolor* (Porfirio *et al.,* 2016 b). The apparent difference between the predominantly diurnal juveniles and the solitary adults observed

in Araucaria forest may be related to a strategy for avoiding predation by *Puma concolor*. Female deer accompanied by juveniles may avoid activity during periods when there is greater risk of predation. Natural predation is of relevance to cervid activity patterns (Long *et al.,* 2013) and human predation influences neotropical cervids (Di Bitetti *et al.,* 2008). Cervids' strategies for protecting their young from predation include synchronized births, among species that inhabit open environments and form large herds, and hiding young that are only a few days old camouflaged in vegetation while the females feed themselves, among species that inhabit environments with cover (Mattioli, 2011). Another strategy is a tendency for young to be born during the afternoon, peaking between 15:00 and 17:00, when predators are less active, as has been observed in *Dama dama* in the Doñana national park in Southeastern Spain (San José & Braza, 1992). The mother's ability to learn is an important factor in selection, since it is linked with her ability to hide or move her young and to detect when predators are abundant, and with perfecting defensive tactics, learning escape routes and accessing food resources (Barber-Meyer & Mech, 2008). The mother's experience is a fundamental element in her young's survival. Younger *Odocoileus virginianus* females lose more of their young than older females (Ozoga & Verme, 1986). Lactating females significantly modify their behavior in terms of selection of habitat and size of living area, in comparison with females that are not lactating (Bongi *et al.,* 2008).

The activity pattern of *Puma concolor* during the summer extended to last the whole night and was slightly different from reports in other studies. This is a species with a wide geographical distribution (Sunquist & Sunquist, 2002) that lives in a range of very different environments. It has been considered a cathemeral species with peak activity at the start of the morning (r = 0.12) in subtropical semideciduous forest (Di Bitetti *et al.,* 2010), in Amazonian pre-Andean seasonal forest (Gómez *et al.,* 2005) and in the Pantanal wetlands (Oliveira, 1994; Porfirio *et al.,*2016 b), but was found to be preponderantly nocturnal in a transition environment between Amazonian forest, Cerrado savannah and secondary forest (Negrões *et al.*, 2011).

Leopardus pardalis exhibits basically nocturnal behavior, but has also been observed active by day in some of the forest environments it inhabits (Gómez *et al.*, 2005;Maffei *et al.*, 2005; Kasper *et al.*, 2007; Di Bitetti *et al.*, 2010; Jiménez *et al.,* 2010; Negrões *et al.*, 2011; Salvador & Espinosa, 2015; Blake *et al.*, 2016; Torre *et al.*, 2016) The results of the present study revealed activity throughout the entire night, with peaks before midnight and after midnight, bearing out reports of 12 to 14 hours' activity per night, with reduced activity after daybreak and until the end of the afternoon, becoming active once more between one and two hours before nightfall (Sunquist & Sunquist, 2002). Just as significant differences in the activity patterns of ocelots across different seasons could not be detected in

Araucaria forest, no differences between activity during the wet and dry seasons were detected in the Pantanal (Porfirio *et al.,* 2016 a).

Leopardus tigrinus or *L. guttulus* as Trigo *et al.,* 2013 have reclassified it, exhibits a cathemeral activity pattern, confirming the observations of other studies (Oliveira *et al.,* 2006), and has peak activity at the start of the morning, as has also been described in Argentina (Di Bitetti *et al.,* 2010). Of all the felines recorded in the FLONASFP, this was the species with the greatest daily activity plasticity. *Leopardus tigrinus* exhibited seasonal alternation between a tendency to a diurnal pattern (Spring) and activity throughout the 24 hours, one of the basic forms of cathemerality (Tattersall, 2006).

Cerdocyon thous exhibited a basically crepuscular activity pattern, which is not always the case in studies of this species. *Cerdocyon thous* is generally considered to be nocturnal (Berta, 1982; Kasper *et al.,* 2007; Negrões *et al.,* 2011) or nocturnal with crepuscular peaks of activity (Jácomo *et al.,* 2004; Di Bitetti *et al.,* 2009; Faria-Corrêa *et al.,* 2009). However, the way that some studies classified periods of the day means it is not possible to investigate the proportion of activity in nocturnal and crepuscular periods, because they split the twilight hours half and half between day and night. The species has also been considered cathemeral (Tortato & Althoff, 2009). Another issue related to the different chrono-ecotype classifications is a lack of uniformity with relation to defining the crepuscular period and a clear

delimitation in time depending on region studied and time of year. This is why the proposal made by Theuerkauf *et al.,* 2003, that two hours around sunrise and sunset should be defined as the crepuscular period, is a good option, because it takes more appropriate account of the photoperiods throughout the year in different regions, making comparisons more precise.

The majority of records of *Dasyprocta azarae* were during the diurnal period, followed by the crepuscular period. This species has been observed to display a diurnal activity pattern in seasonal semidecidual forest (Kasper *et al.,* 2007) and diurnal to crepuscular in areas of transition between Cerrado savannah and Amazonian forest (Negrões *et al.,* 2011). In the Pantanal, this species was diurnal during the wet season and diurnal with crepuscular peaks of activity during the dry season (Porfirio *et al.,* 2016 a). Other species belonging to the same genus have a diurnal pattern with peaks also during twilight hours (Gómez *et al,.* 2005; Lambert *et al.,* 2009; Norris *et al.,* 2010) The last of these studies interpreted the increased crepuscular activity as a strategy for avoiding the more intense midday heat and more active predators (ocelots) at night, while nocturnal activity had a positive relationship with the availability of fruit. In the Pantanal, agoutis were less active close to midday on hotter days and increased their activity later on during the afternoon, maintaining overall activity constant in relation to days with lower temperatures (Cid *et al.,* 2015). In the Atlantic forest in Southeast Brazil, agouti exhibited

activity peaks (in the morning and afternoon) and there were no records of activity during the hottest period of the day, from 12:00 to 13:30 (Ferreguetti *et al.,* 2018). This pause in activity close to midday was observed in all seasons of the year in this study. Apparently agoutis reduce activities involving displacement at the end of the morning. In mixed rain forest, the greatest peaks of activity occurred around dusk and dawn and there was activity at all times of day, while the majority of nocturnal records were during autumn and winter. During the winter, *Araucaria angustifolia* (Brazilian pine) is responsible for producing more than 90% of the fruit and seeds in this community, since its seeds (pinhões) are large (6.5 – 8.5 g), highly nutritious and ripen between April and July (Vieira et al., 2011). There are a number of photographic records of agoutis carrying Araucaria seeds (pinhões) in their mouths during the season when these seeds are available, which occurs exactly when environmental temperatures are lowest and, in principle, greater energy consumption is needed to maintain metabolism. Activity times in the winter were significantly different from all of the other three seasons, with greater intensity of activity observed at the end of the afternoon than during the day. This finding indicates that the ambient temperature is probably not the most important factor stimulating the activity of agoutis, since it was exactly in the season with the lowest temperatures that this species was proportionally less active during the day. However, availability of good quality food is an important factor affecting daily activity

(Bourgoin et al., 2008).

Studies of mammal assemblages must be conducted at all times of day in order to avoid observation bias towards any given period. The differences in times of activity observed for some species of medium and large mammals in Araucaria forest during different seasons indicate adaptation to an environment in which temperatures oscillate greatly, but where the differences are not as extreme as in temperate environments. Studies of neotropical mammals must compare assemblages living in different natural environments in order to detect distinct behavioral patterns to of adaptation to the challenges of survival.

References

Ancona, K.A. & Loughry, W.J. 2009. Time budgets of wild nine-banded armadillos. **Southeastern Naturalist 8**(4): 587-598.

Ando, C. 2003. The relationship between deer-train collisions and daily activity of the sika deer, *Cervus nippon.* **Mammal Study 28**: 135-143.

Arispe, R.; Venegas, C. & Rumiz, D. 2008. Abundancia y patrones de actividad del mapache (*Procyon cancrivorus*) en un bosque chiquitano de Bolivia. **Mastozoologia Neotropical 15**(2): 323-333.

Barber-Meyer, S.M. & Mech, L.D. 2008. Factors influencing predation on juvenils ungulates and natural selection implications. **Wildlife Biology in Practice 4**(1):8-29.

Berta, A. 1982. *Cerdocyon thous.* **Mammalian Species** (186): 1-4.

Blake, J.G.; Mosquera, D.; Loiselle, B.A.; Swing, K.; Guerra, J. & Romo, D. 2016. Spatial and temporal activity patterns of ocelots *Leopardus pardalis* in lowland forest of Eastern Ecuador. **Journal of Mammalogy 97**(2):455-463.

Bongi, P.; Ciuti, S.;Grignolio, S.; Frate, M.D.e.l; Simi, S.; Gandelli, D. & Apollonio, M. 2008. Anti-predator behaviour, space use and habitat selection in female roedeer during the fawning season in a wolf area. **Journal of Zoology 276**: 242-251.

Bourgoin, G.; Garel, M.; Moorter, B.V.a.n; Bubray, D.; Maillard, D.; Marty, E. & Gaillard, J.M. 2008. Determinants of seasonal variation in activity patterns of mouflon. **Canadian Journal of Zoology 86:** 1410-1418.

Cademartori, C.V.; Marques, R.V.; Pacheco, S.M.; Baptista, L.R.M. & Garcia, M. 2002. Roedores ocorrentes em Floresta Ombrófila Mista (São Francisco de Paula, Rio Grande do Sul) e a caracterização de seu hábitat. **Comunicações do Museu de Ciências e Tecnologia PUCRS, Sér. Zoologia 151**: 61-86.

Carver, B.D.; Kennedy, M.L.; Houston, A.E. & Franklin, S.B. 2011. Assessment of temporal partitioning in foraging patterns of syntopic Virginia opossums and raccoons. **Journal of Mammalogy 92**(1): 134-139.

Castro-Arellano, I. & Lacher Jr., T.E. 2009. Temporal niche segregation in two rodent assemblages of subtropical Mexico. **Journal of Tropical Ecology 25**: 593-603.

Chiarello, A.G. 2000. Density and population size of mammals in remnants of Brazilian Atlantic Forest. **Conservation Biology 14**(6): 1649-1657.

Cid, B.; Oliveira-Santos, L.G.R. & Mourão, G. 2015. The relationship between external temperature and daily activity in a large rodent (*Dasyprocta azarae*) in the Brazilian Pantanal. **Journal of Tropical Ecology 31**(5): 469-472.

Cuellar, E.; Maffei, L.; Arispe, R. & Noss, A. 2006. Geoffroy's cats at the northern limit of their range: activity patterns and density estimates from camera trapping in Bolivian dry forests. **Studies on Neotropical Fauna and Environment 41**(3): 169-177.

Daan, S. & Aschoff, J. 1975. Circadian rhythms of locomotor activity in captive birds and mammals: their variations with season and latitude. **Oecologia 18**: 269-316.

Decoursey, P.J. 2004. Diversity of function of SNC pacemakers in behavior and ecology of three species of sciurid rodents. **Biological**

Rhythm Research 35: 13-33.

DI BITETTI, M.S.; DE ANGELO, C.D.; DI BLANCO, Y.E. & PAVIOLO, A. 2010. Niche partitioning and species coexistence in a Neotropical felid assemblage. **Acta Oecologica 36**(4): 403-413.

DI BITETTI, M.S.; DI BLANCO, Y.E.; PEREIRA, J.A.; PAVIOLO, A. & PÉREZ, I.J. 2009. Time partitioning favors the coexistence of sympatric crab-eating foxes (*Cerdocyon thous*) and Pampas foxes (*Lycalopex gymnocercus*). **Journal of Mammalogy 90** (2): 479-490.

DI BITETTI, M.S.; PAVIOLO, A. & DE ANGELO, C. 2006. Density, habitat use and activity patterns of ocelots (*Leopardus pardalis*) in the Atlantic Forest of Misiones, Argentina. **Journal of Zoology 270:** 153-163.

DI BITETTI, M.S.; PAVIOLO, A.; FERRARI, C.A.; DE ANGELO, C. & DI BLANCO, Y. 2008. Differential responses to hunting in two sympatric species of brocket deer (*Mazama americana* and *M. nana*). **Biotropica 40**(5): 636-645.

DUARTE, J.M.B. 1996. **Guia de identificação de cervídeos brasileiros.** Jaboticabal, FUNEP, 14p.

ERKERT, H.G.; BAY, F.A. & KRACHT, S. 1976. Zeitgeber induced modulation of activity patterns in nocturnal mammals (Chiroptera). **Experientia 32**(5): 560-562.

FARIA-CORRÊA, M.; BALBUENO, R.A.; VIEIRA, E.M. & FREITAS, T.R.O. 2009. Activity, habitat use, density, and reproductive biology of the crab-eating fox (*Cerdocyon thous*) and comparison with the pampas fox (*Lycalopex gymnocercus*) in a Restinga area in the southern Brazilian Atlantic Forest. **Mammalian Biology 74**: 220-229.

FAUTH, J.E.; BERNARDO, J.; CAMARA, M.; RESETARITS JR., W.J.; BUSKIRK, J. VAN & McCOLLUM, S.A. 1996. Simplifying the jargon of community ecology: a conceptual approach. **The American Naturalist 147**: 282-286.

FERREGUETTI, A.C.; TOMAS, W.M. & BERGALLO, H.G. 2018. Density, habitat use, and daily activity patterns of the Red-rumped Agouti (*Dasyprocta leporina*) in the Atlantic Forest, Brazil. **Studies on Neotropical Fauna and Environment** DOI: 10.1080/01650521.2018.1434743

GALLIEZ, M.; LEITE, M.S.; QUEIROZ, T.L. & FERNANDEZ, F.A.S. 2009. Ecology of the water opossum *Chironectes minimus* in Atlantic Forest streams of southeastern Brazil. **Journal of Mammalogy 90**(1): 93-103.

GEORGII, B. & SCHRÖDER, W. 1983. Home range and activity patterns of male red deer (*Cervus elaphus* L.) in the alps. **Oecologia 58:** 238-248.

GÓMEZ, H.; WALLACE, R.B.; AYALA, G. & TEJADA, R. 2005. Dry season activity periods of

some Amazonian mammals. **Studies on Neotropical Fauna and Environment 40**(2): 91-95.

HICKS, N.G.; MENZEL, M.A. & LAERM, J. 1998. Bias in the determination of temporal activity patterns of syntopic *Peromyscus* in the southern Appalachians. **Journal of Mammalogy 79**(3): 1016-1020.

JÁCOMO, A.T.A.; SILVEIRA, L. & DINIZ-FILHO, J.A.F. 2004. Niche separation between the maned wolf (*Chrysocyon brachyurus*), the crab-eating fox (*Dusicyon thous*) and the hoary fox (*Dusicyon vetulus*) in central Brazil. **Journal of Zoology 262**: 99-106.

JIMÉNEZ, C.F.; QUINTANA, H.; PACHECO, V.; MELTON, D.; TORREALVA, J. & TELLO, G. 2010. Camera trap survey of medium and large mammals in a montane rainforest of northern Peru. **Revista Peruana de Biologia 17**(2): 191-196.

KASPER, C.B.; MAZIM, F.D.; SOARES, J.B.G.; OLIVEIRA, T.G. & FABIÁN, M.E. 2007. Composição e abundância relativa dos mamíferos de médio e grande porte no Parque Estadual do Turvo, Rio Grande do Sul. **Revista Brasileira de Zoologia 24**(4): 1087-1100.

KITCHEN, A.M.; GESE, E.M. & SCHAUSTER, E.R. 2000. Changes in coyote activity patterns due to reduced exposure to human persecution. **Canadian Journal of Zoology 78**: 853-857.

KOVACH, W.L. 2009. Oriana–Circular Statistics for Windows, ver. 3 Kovach Computing Services, Pentraeth, Wales, U.K. Available on line at: **http://www.kovcomp.com/oriana/oribroc.html** Accessed: 12 mar. 2011.

KOVACH, W.L. 2011. Oriana–Circular Statistics for Windows, ver.4. Kovach Computing Services, PENTRAETH, WALES, U.K. Available on line at: **http://www.kovcomp.com/oriana/index.html** Accessed: 31 dec. 2014.

KRONFELD-SCHOR, N. & DAYAN, T. 2003. Partitioning of time as an ecological resource. **Annual Review of Ecology, Evolution and Systematics 34**: 153-181.

LAMBERT, T.D.; KAYS, R.W.; JANSEN, P.A.; ALIAGA-ROSSEL, E. & WIKELSKI, M. 2009. Nocturnal activity by primarily diurnal Central American agouti (*Dasyprocta punctata*) in relation to environmental conditions, resource abundance and predation risk. **Journal of Tropical Ecology 25**: 211-215.

LARRUCEA, E.S. & BRUSSARD, P.F. 2009. Diel and seasonal activity patterns of pygmy rabbits (*Brachylagus idahoensis*). **Journal of Mammalogy 90**(5): 1176-1183.

LEHNER, P.N. 1996. **Handbook of Ethological Methods.** 2.ed. Cambridge, Cambridge Univ. Press, 672p.

LEITE, M.S.; QUEIROZ, T.L.; GALLIEZ, M.; MENDONÇA, P.P. & FERNANDEZ, F.A.S. 2013. Activity patterns of the water opossum *Chironectes minimus* in Atlantic Forest Rivers of south-eastern Brazil. **Journal of Tropical Ecology**

29(3): 261-264.

LONG, E.S.; JACOBSEN, T.C.; NELSON, B.J. & STEENSMA, K.M.M. 2013. Conditional daily and seasonal movement strategies of male Columbia black-tailed deer (*Odocoileus hemionus columbianus*). **Canadian Journal of Zoology 91:** 679-688.

LOUGHRY, W.J. & MCDONOUGH, C.M. 1998. Comparisons between nine-banded armadillo (*Dasypus novemcinctus*) populations in Brazil and the United States. **Revista de Biologia Tropical 46**(4): 1173-1183.

MAFFEI, L.; NOSS, A.J.; CUÉLLAR, E. & RUMIZ, D.I. 2005. Ocelot (*Felis pardalis*) population densities, activity, and ranging behaviour in the dry forests of eastern Bolívia: data from camera trapping. **Journal of Tropical Ecology 21**: 349-353.

MARQUES, M.D. 2004. Rhythms and Ecology–Do chronobiologists still remember nature? **Biological Rhythm Research 35**: 1-2.

MARQUES, R.V.; CADEMARTORI, C.V. & PACHECO, S.M. 2011. Mastofauna no Planalto das Araucárias, Rio Grande do Sul, Brasil. **Revista Brasileira de Biociências 9** (3): 278-288.

MARQUES, R.V. & MAZIM, F.D. 2005. A utilização de armadilhas fotográficas para o estudo de mamíferos de médio e grande porte. **Caderno La Salle XI,** Canoas **2** (1): 219-228.

MARQUES, R.V. & RAMOS, F.M. 2001. Identificação de mamíferos ocorrentes na Floresta Nacional de São Francisco de Paula/IBAMA, RS com a utilização de equipamento fotográfico acionado por sensores infravermelhos. **Divulgações do Museu de Ciências e Tecnologia, UBEA/PUCRS** (6): 83-94.

MATTIOLI, S. 2011. Family Cervidae. p.350-443. In: WILSON, D.E. & MITTERMEIER, R.A. (eds). **Handbook of the Mammals of the World.** V.2. Hoofed Mammals. Barcelona, Lynx Edicions. 885p.

MCBEE, K. & BAKER, R.J. 1982. *Dasypus novemcinctus.* **Mammalian Species** (162): 1-9.

MCDONOUGH, C.M. & LOUGHRY, W.J. 1997. Influences on activity patterns in a population of nine-banded armadillos. **Journal of Mammalogy 78**(3): 932-941.

MICHALSKI, F. & NORRIS, D. 2011. Activity pattern of *Cuniculus paca* (Rodentia: Cuniculidae) in relation to lunar illumination and other abiotic variables in the southern Brazilian Amazon. **Zoologia 28**(6): 701-708.

MONROY-VILCHIS, O.; ZARCO-GONZÁLEZ, M.M.; RODRÍGUEZ-SOTO, C.; SORIA-DÍAZ, L. & URIOS, V. 2011. Fototrampeo de mamíferos en la Sierra Nanchititla, México: abundancia relativa y patrón de actividad. **Revista de Biología Tropical 59**(1): 373-383.

MORGAN, E. 2004. Ecological significance of

biological clocks. **Biological Rhythm Research 35**(1/2): 3-12.

Negrões, N.; Revilla, E.; Fonseca, C.; Soares, A.M.V.M.; Jácomo, A.T.A. & Silveira, L. 2011. Private Forest reserves can AID in preserving the community of medium and large-sized vertebrates in the Amazon arc of deforestation. **Biodiversity and Conservation 20**: 505-518.

Norris, D.; Michalski, F. & Peres, C.A. 2010. Habitat patch size modulates terrestrial mammal activity patterns in Amazonian Forest fragments. **Journal of Mammalogy 91**(3): 551-560.

Observatório Nacional, 2011. Anuário Interativo do Observatório Nacional. Available on line at: **http://euler.on.br/ephemeris/index.php** Accessed: 31 jan. 2011.

Oliveira, T.G. 1994. **Neotropical Cats: ecology and conservation.** São Luiz, EDUFMA, 220p.

Oliveira, T.G.; Tortato, M.A.; Kasper, C.B.; Marques, R.V.; Marques, M.C. & Cassaro, K. 2006. Little spotted cat in Brazil. **Wild Cat News 2**(3): 1-5.

Oliveira-Santos, L.G.R.; Machado-Filho, L.C.P.; Tortato, M.A. & Brusius, L. 2010. Influence of extrinsic variables on activity and habitat selection of lowland tapirs (*Tapirus terrestris*) in the coastal sand plain shrub, southern Brazil. **Mammalian Biology 75**: 219-226.

Oliveira-Santos, L.G.R.; Tortato, M.A. & Graipel, M.E. 2008. Activity pattern of Atlantic Forest small arboreal mammals as revealed by camera traps. **Journal of Tropical Ecology 24**: 563-567.

Ozoga, J.J. & Verme, L.J. 1986. Relation of maternal age to fawn-rearing success in white-tailed deer. **The Journal of Wildlife Management 50**: 480-486.

Pita, R.; Mira, A. & Beja, P. 2011. Circadian activity rhythms in relation to season, sex and interspecific interactions in two Mediterranean voles. **Animal Behaviour 81:** 1023-1030.

Porfirio, G.; Foster, V.C.; Fonseca, C. & Sarmento, P. 2016 a. Activity patterns of ocelots and their potential prey in the Brazilian Pantanal. **Mammalian Biology 81**: 511-517.

Porfirio, G.; Sarmento, P.; Foster, V. & Fonseca, C. 2016 b. Activity patterns of jaguars and pumas and their relationship to those potential prey in the Brazilian Pantanal. **Mammalia 81**(4): 401-404.

Rivero, K.; Rumiz, D.I. & Taber, A.B. 2005. Differential habitat use by two sympatric brocket deer species (*Mazama americana* and *M. gouazoubira*) in a seasonal Chiquitano forest of Bolivia. **Mammalia 69**(2): 169-183.

Salvador, J. & Espinosa, S. 2015. Density and activity patterns of ocelot populations in

Yasuní National Park, Ecuador. **Mammalia 80**(4): 395-403.

San José, C. & Braza, E. 1992. Anti-predator aspects of fallow deer behavior during calving seasons at Doñana National Park (Spain). **Ethology, Ecology & Evolution 4**: 139-149.

Schwitzer, N.; Kaumanns, W.; Seitz, P.C. & Schwitzer, C. 2007. Cathemeral activity patterns of the blue-eyed Black lemur *Eulemur macaco flavifrons* in intact and degraded forest fragments. **Endangered Species Research 3**: 239-247.

SOS Mata Atlântica & INPE - Instituto Nacional de Pesquisas Espaciais. 2010. Atlas dos Remanescentes Florestais da Mata Atlântica: período 2008-2010. Available on line at: **http://www.mapas.sosma. org.br/site_media/download/atlas-relatorio2008-2010parcial.pdf.** Accessed: 19 jul. 2010.

Sunquist, M. & Sunquist, F. 2002. **Wild Cats of the World.** Chicago, Univ. Chicago Press, 452p.

Tattersall, I. 2006. The concept of cathemerality: history and definition. **Folia Primatologica 77**: 7-14.

Theuerkauf, J.; Jedrzejewski, W.; Schmidt, K.; Okarma, H.; Ruczynski, I.; Sniezko, S. & Gula, R. 2003. Daily patterns and duration of wolf activity in the Bialowieza Forest, Poland. **Journal of Mammalogy 84**(1): 243-253.

Torre, A. de la; Arroyo-Gerala, P. & Torres-Knoop, L. 2016. Density and activity patterns of ocelot in the Greater Lacandona Ecosystem. **Therya 7**(2): 257-269.

Tortato, F.R. & Althoff, S.L. 2009. Avaliação de fatores abióticos sobre o período de atividade do graxaim (*Cerdocyon thous* Carnivora: Canidae). **Biotemas 22**(4): 147-152.

Trigo, T.C.; Schneider, A.; Oliveira, T.G; Lehugeur, L.M.; Silveira, L.; Freitas, T.R.O. & Eizirik, E. 2013. Molecular data reveal complex hybridization and a cryptic species of Neotropical wild cat. **Current Biology 23**(24): 2528-2533.

Vanderhoff, E.N.; Hodge, A.M.; Arbogast, B.S.; Nilsson, J. & Knowles, T.W. 2011. Abundance and activity patterns of the margay (*Leopardus wiedii*) at a mid-elevation site in the eastern Andes of Ecuador. **Mastozoología Neotropical 18**(2): 271-279.

Vieira, E.M.; Baumgarten, L.C.; Paise, G. & Becker, R.G. 2010. Seasonal patterns and influence of temperatura on the daily activity of the diurnal neotropical rodent *Neocromys lasiurus.* **Canadian Journal of Zoology 88**: 259-265.

Vieira, E.M.; Ribeiro, J.F. & Iob, G. 2011. Seed predation of *Araucaria angustifolia* (Araucariaceae) by small rodents in two

areas with contrasting seed densities in the Brazilian Araucaria forest. **Journal of Natural History 45**(13-14): 843-854.

WECKEL, M.; GIULIANO, W. & SILVER, S. 2006. Jaguar (*Panthera onca*) feeding ecology: distribution of predator and prey through time and space. **Journal of Zoology 270:** 25-30.

WILSON, D. E. & REEDER, D.M. 2005. **Mammal Species of the World:** A Taxonomic and Geographic Reference. 3ed. Baltimore, Johns Hopkins, 2142p.

ZAR, J.H. 2010. **Biostatistical Analysis.** 5ed. Upper Saddle River, Prentice Hall, 944p.