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Daily rhythmicity of behavior of nine species of South American feral felids in captivity

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Abstract

The authors analyzed the daily activity rhythms of the domestic cat and of eight of the ten feral felid species that are indigenous to South America. All species showed daily rhythmicity of activity in captivity under a natural light-dark cycle. The robustness of the rhythmicity varied from species to species, but the grand mean of 34% was within the range of robustness previously described for mammalian species ranging in size from mice to cattle. There was not a sharp division between diurnal and nocturnal felids. Instead, what was found was a gradient of diurnality going from the predominantly nocturnal margay (72% of activity counts during the night) to the predominantly diurnal jaguarundi (87% of activity counts during the day) with the remaining species lying in between these two extremes. The ecological implications of temporal niche variations are discussed.

Keywords: circadian rhythm, locomotor activity, *Felis catus*, *Leopardus colocolo*, *Leopardus geoffroyi*, *Leopardus pardalis*, *Leopardus tigrinus*, *Leopardus guttulus*, *Leopardus wiedii*, *Panthera onca*, *Puma concolor*, *Puma yagouaroundi*

1. Introduction

The temporal distribution of an animal's activity over the cycle of day and night and over the alternation of the seasons is of great importance for reproductive success [1-3] and survival of the species [4-6]. The need to forage efficiently while avoiding predators leads to a trade-off between starvation and predation risk that can affect the proportion of time per day allocated to activity and to foraging as well as the timing and alternation of these processes [7-9]. Full understanding of the daily activity rhythm of a species is, therefore, of paramount importance for the understanding of the biology of the species.

The daily distribution of locomotor activity has been studied in numerous mammalian species [10-12], but few studies have been conducted on felids. A few general studies of activity rhythms have been conducted on felids in the wild [13-15] and in captivity [16-18], but detailed studies on various species have yet to be accomplished. We describe here a detailed analysis of the daily activity rhythms of the domestic cat and of eight of the ten feral felid species that are indigenous to South America [19], which belong to three different genera (*Panthera*, *Puma*, and *Leopardus*) and have different life styles in terms of active times, social structure, maternal investment, etc. The Pampas cat (*Leopardus colocolo*), Geoffroy's cat (*Leopardus geoffroyi*), ocelot (*Leopardus pardalis*), oncilla (*Leopardus tigrinus/guttulus*), margay (*Leopardus wiedii*), and jaguar (*Panthera onca*) are considered to be in danger of extinction in the wild, whereas the puma (*Puma concolor*) and jaguarundi (*Puma yagouaroundi*) are not currently endangered but require controlled commercial exploitation [20].

The distribution of body sizes of South American felids is unique. Two species are large felids (heavier than 15 kg): the jaguar and puma. One is intermediate: the ocelot. The remaining species are small (lighter than 7 kg): the Andean mountain cat, Geoffrey's cat, guiña, jaguarundi, margay, oncilla, and Pampas cat. The ecological characteristics of South American felids also delineate three groups. The first one is composed of specialist species associated with one or a few ecoregions (jaguar, guiña, and Andean mountain cat); the second group comprises species that are less specialized and have broader distributions (ocelot, margay, and oncilla); and the third group contains generalist species with broad geographical distribution (puma, jaguarundi, Geoffrey's cat, and Pampas cat) [21].

Argentina is the only country in the continent in which all ten species of feral South American felids can be found [22]. Two of these species (Andean cat and guiña) are not found in captivity in any animal facility in the country [21]. The others can be found in captivity in varied numbers, depending on the species and origin of the specimens. Most of these animals are not part of exhibits; instead, they enter rehabilitation centers because of illegal possession, illegal traffic, run-overs, or natural disasters, and are returned to their habitats after rehabilitation, except for large felines (jaguar and puma), whose release is limited because of danger to humans and cattle [23]. Yet, the jaguar in Argentina is critically endangered, with fewer than 250 adults remaining in the wild and 14 in zoological parks.

The domestic cat (*Felis catus*) was domesticated thousands of years ago and can be found in captivity or in the feral state all over the world [24]. Its daily distribution of activity is generally described as poorly structured with a slight preference for nocturnal activity both in the wild [25] and in the laboratory [26]. This species was included in the study because, although it is not originally from South America, it is currently found throughout South America, sometimes in the feral state.

The Pampas cat is described as having a preference for habitats characterized by grasslands, shrubs, and bushes [27]. It shares this habitat with the jaguarundi, Geoffroy's cat, and

Andean cat. It is reported to be solitary and crepuscular in grasslands in Brazil but nocturnal in the Andes and feeds mostly on birds [21].

The Geoffroy's cat is generally nocturnal and is a good climber. It is a common predator of farmed birds and small prey [21].

The ocelot is described as nocturnal, covering about 8 km while foraging each night [22], but diurnal when not challenged by natural predators [21], often being active either during the day or during the night [28]. It is a good swimmer and climber, feeding on small mammals, reptiles, amphibians, fishes, and crabs.

The margay is solitary and apparently nocturnal [29]. It feeds on a variety of animal species, predominantly arboreal ones. To avoid direct sun exposure, it hides high in tree canopies or tree cavities [21].

The oncilla, traditionally considered to be a single species (*Leopardus tigrinus*), seems to encompass three distinct species, the one found in Argentina most likely being *Leopardus guttulus* [30]. It shares mountain forests and Andean moors with the puma and lowlands with the jaguar, puma, ocelot, jaguarundi, and margay [31]. It tends to be terrestrial, solitary, territorial, and possibly nocturnal [21].

The jaguarundi is a flexible species, being found both in open areas (savannahs and floodplains) and in wooded areas, preferentially near water streams. It is reported to be diurnal, exhibiting bouts of 4 to 11 hours of continual activity [21].

The puma seems to be crepuscular and nocturnal. It is solitary, sedentary, and territorial. It is a good runner and climber. When food is scarce, it becomes more aggressive and may attack humans beings [21].

The jaguar is reported to hunt at dawn and to rest during the rest of the day [21]. It moves on land and in water, hunting mammals, birds, reptiles, and fishes. It also predates on other carnivores. About 60% of its prey are relatively large (weighing more than 15 kg). It is dangerous to humans, both in the wild and in captivity [32].

The detailed analysis of behavioral activity of these species that is reported here complements the knowledge obtained by observations of behavior in the wild. The results are valuable not only as an addition to the natural history of South American felids but also as practical information to assist zoological parks and rehabilitation agencies in providing adequate care for these and related animals.

2. Materials and method

2.1. Subjects

All animals used as subjects in this study were participants in a program of rescue and rehabilitation of feral felids in South America. The nine species are listed in Table 1 along with their mean body masses, sample sizes, study sites, and living-space sizes. The morphometric parameters of each species were within the values reported by Macdonald and Loveridge [30]. Although exact ages of animals born and raised in the wild cannot be determined without invasive procedures, visual examination allowed the determination that, except for the jaguar, all animals were young adults. The jaguar was an older adult (approximately 14 years old).

The study was conducted at four different sites: Estación Biológica Experimental Granja La Esmeralda (Santa Fe, Argentina), Centro de Conservación de Vida Salvaje Güirá Oga (Puerto Iguazú, Argentina), Reserva Ecológica El Puma (Candelaria, Argentina), and Refúgio Biológico

Bela Vista (Foz do Iguaçu, Brazil). The geographical location of these sites is indicated in Fig. 1, which also indicates the historical and current distribution of the various species.

The animals chosen for the study were healthy animals that were approaching the time for return to the wild. Their origin was variable. Some were rescued from multiple locations, some were intercepted during illegal animal traffic, and some were donated to the conservation agencies. All animals had been in captivity for at least a year when the study commenced.

Except for the domestic cat, the various species were housed in their usual living spaces, which had vertical and horizontal structures with various visual barriers (such as shrubs and branches) allowing individuals to evade visual contact with or hide from other animals, such as the living space shown in Fig. 2. Preservation of typical behavior was facilitated by an enrichment program that provided the animals with the opportunity for various feeding strategies (live prey, dead prey, hidden food, water ad libitum, etc.).

Experiments were conducted in accordance with the regulations of the Guidelines for the Use of Wild Mammals in Research (American Society of Mammalogists, 2011) and the Guide for the Care and Use of Laboratory Animals (U.S. National Research Council, 2011).

2.2. Procedure

All felines were housed individually during the study, which consisted of 13 consecutive days under natural conditions of illumination and ambient temperature. A 12L:12D light-dark cycle was secured by restriction of data collection to the time of the year close to the equinoxes. The study sites were located approximately in the center of the geographical distribution of the various species and, therefore, had a representative range of ambient temperatures, particularly during the equinoxes (March average high temperature: 28°C, average low temperature: 18°C). The animals had free access to water and were fed according to the standard procedure at each facility. Feed consisted of fresh beef, poultry meat, or live prey (rats, doves, or quail) provided either once daily or on alternate days.

For the continuous recording of activity, an activity data-logger (Actiwatch, Cambridge Neurotechnology, Cambridge, UK) was strapped to the animal's neck and left in place for the duration of the study. The device monitored the animal's activity by the accelerometer technique and stored data in 30-min intervals for later analysis. Activity was defined as any movement the animal made, including different behaviors such as feeding, drinking, walking, and grooming, independently of the animal's position, such as lying or standing.

2.3. Data analysis

A time interval of 13 consecutive days (624 data points) was analyzed for each individual of each species. Daily wave-form plots of activity were generated for each species by averaging, time-bin by time-bin, the 13 consecutive days for each animal and then averaging all animals in each species while preserving the temporal resolution of the original data sets.

For each individual of each species, three parameters of the activity rhythm were analyzed: acrophase, robustness, and diurnality. The mesor (mean level) and amplitude of the rhythm were not given consideration for two reasons. The first reason is that the activity counts registered by the Actiwatches are not calibrated to reflect distance covered or stationary movement in a reliable manner. The second reason is that the sizes of the living spaces were not rigorously scaled to the sizes or habits of the animals, which means that some species might have been more restricted in their movements than other species. Thus, the analysis of mesor and amplitude could not produce valid interspecies comparisons in this study.

Acrophase is the time of the daily peak of the activity rhythm. The acrophase was computed by the single cosinor procedure, which fits a cosine wave to the data in order to overcome differences in wave form of the time series under analysis [34, 35]. This is particularly important when different species are being compared, as the wave form of the activity rhythm is known to vary greatly from species to species. The acrophase computed by the cosinor procedure provides a "center-of-gravity" measure of the wave form that minimizes the effects of differences in slope, bimodality, etc. [35].

The second parameter of the activity rhythm to be analyzed was rhythm robustness. Rhythm robustness refers to the strength of rhythmicity and is closely related to the stationarity of the time series [36]. Robustness is independent of amplitude, except at the extreme low end of the range, as a rhythm with zero amplitude also has zero robustness. Rhythm robustness was computed as the Q_P value of the chi-square periodogram statistic as a percentage of the maximal Q_P value for the data set [36].

The third parameter to be analyzed was diurnality. A diurnality index was calculated for each individual by dividing the total activity counts accumulated during the light phase of the daily cycle by the activity counts accumulated during the whole day and multiplying the result by 100.

The statistical significance of differences between group means was evaluated by analysis of variance (ANOVA) followed by post-hoc pairwise comparisons with Tukey's HSD test [37]. The level of significance ($\alpha = 0.05$) was maintained at each ANOVA.

3. Results

A nine-day segment of the records of activity of a representative Geoffroy's cat is presented in Fig. 3. Activity shows clear daily rhythmicity, with movement being recorded mostly during the night. Although there is clear day-to-day variability, the activity rhythm is quite strong. This animal exhibited acrophase at 00:20 (that is, with peek activity 20 min after midnight), rhythm robustness of 45% (that is, a moderately robust activity rhythm), and diurnality of 26% (that is, a predominantly nocturnal activity pattern).

Daily wave-form plots of activity of each of the nine species are shown in Fig. 4. Whereas all individual felines exhibited statistically significant 24-hour rhythmicity of activity, as determined by the cosinor test ($p < 0.001$), different species exhibited different activity patterns. Perhaps most noticeable in the figure is the concentration of activity during the night in species such as the margay and Geoffroy's cat, the concentration of activity during the day in species such as the jaguarundi and jaguar, and more complex patterns in the other species. The average activity pattern for the pumas has an arrhythmic appearance because of relatively high inter-individual variability in this species (meaning that individual animals exhibited daily rhythmicity of behavior, but some individuals tended to be diurnal whereas others tended to be nocturnal).

The interspecies differences noted in Fig. 4 are quantified in Fig. 5 in terms of acrophase, rhythm robustness, and diurnality. To allow the inclusion of all species in a global analysis of variance, three separate data sets were used from each of the single individuals of Pampas cat and jaguar. Analysis of variance indicated the presence of significant differences in the acrophases of the various species ($F_{8,41} = 61.105$, $p < 0.001$). Three species had peak activity shortly after midnight (margay, Geoffroy's cat, and puma), two species shortly after sunrise (domestic cat and Pampas cat), two species around noon (jaguarundi and jaguar), and two species early in the night (oncilla and ocelot).

Also depicted in Fig. 5 are the means of rhythm robustness (strength of rhythmicity). Analysis of variance indicated the presence of significant differences in the robustness of the various species ($F_{8,41}$ = 4.280, p < 0.001), even though the differences were not as marked (ω^2 = 0.31) as those for the acrophase (ω^2 = 0.91). The lowest robustness (18%) was observed in the jaguar, whereas the highest robustness (51%) was observed in the jaguarundi.

The third panel in Fig. 5 shows the means of the diurnality index. Analysis of variance indicated the presence of significant differences in the diurnality of the various species ($F_{8,41}$ = 19.776, p < 0.001). Not surprisingly, variations in the diurnality index were closely correlated with variations in the acrophase expressed in terms of hours since sunset (r = 0.91, p = 0.001). The most diurnal species were the jaguarundi and jaguar, whereas the most nocturnal (least diurnal) species was the margay.

4. Discussion

All species showed daily rhythmicity of activity in captivity under a natural light-dark cycle and mild environmental temperature characteristic of the equinoxes. The robustness of the rhythmicity varied from species to species, but the grand mean of 34% was within the range of robustness previously described for 16 mammalian species ranging in size from mice to cattle [38].

As previously shown for small rodents [39], we did not find a sharp division between diurnal and nocturnal felids. On the contrary, we found a gradient of diurnality going from the predominantly nocturnal margay to the predominantly diurnal jaguarundi with the remaining species spread out between these two extremes. Although the most nocturnal felid in our study (margay: 28% diurnal) was not as nocturnal as some rodents (golden hamster: 0% diurnal [39]), the most diurnal felid (jaguarundi: 87%) was just as diurnal as the most diurnal rodent in the previous study (Nile grass rat: 87% diurnal [39]). As expected, the diurnality of a species was correlated with its acrophase (r = 0.91), so that predominantly nocturnal species had acrophases during the night, and predominantly diurnal species had acrophases during the day.

When different species are in competition in the same area and there are strong selective forces [40], the temporal segregation of the daily activity patterns can potentially be the most effective mechanism to reduce competition [41]. Species with flexible daily rhythmicity (cathemeral species) may be able to adjust their activity pattern to local conditions (predation risk, competitors, or prey) and increase their fitness. This could be specifically beneficial for a generalist predator like the puma, which consumes a broader variety of prey, including diurnal and nocturnal prey [42]. Similarly to what was observed by Di Bitetti and colleagues [43], three of the species in our study (oncilla, puma, and ocelot) showed a cathemeral pattern of activity, as characterized by relatively low rhythm robustness and a diurnality index close to 50%. The jaguar also exhibited low robustness but had a diurnality index above 70%. The temporal separation in the activities of the puma and the jaguar may reflect a strategy of avoidance of direct contact between these two species to allow their coexistence in the same geographical area [44]. There have been previous reports of such temporal separation of sympatric species with similar feeding habits to prevent competition [45].

Field observations at the Kaa Iya National Park, in Bolivia, characterized the jaguar as a predominantly diurnal felid [46], which is in agreement with our findings. On the other hand, two other groups characterized the jaguar as a nocturnal species [47, 48]. Regarding ocelots, Di Bitetti and colleagues [43] noted, as we did, a predominantly nocturnal activity pattern.

The jaguarundi and the margay, which Kiltie described as having the greatest morphological overlap [49], had the most extreme difference in the diurnality index in our study, as the jaguarundi was the most diurnal species (88% diurnal) and the margay was the most nocturnal species (28% diurnal). The margay has strong adaptations for an arboreal and nocturnal lifestyle [50], and these characteristics may reduce competition with the similarly sized jaguarundi and the oncilla, the latter one with a more terrestrial habit and a cathemeral activity pattern, which allows for a flexible use of the temporal axis in response to local competitive conditions.

We found that Geoffroy's cats are mostly active during crepuscular and nocturnal hours, which is consistent with field observations of their hunting behavior [51, 52] and studies in captivity [53]. Nocturnality in small- and medium-sized felids has been attributed to their specialization in catching nocturnal rodents [54, 55]. Small nocturnal rodents are the major component (up to 94%) of the Geoffroy's cat diet in Lihue Calel [56, 57]. Domestic cats have been domesticated for thousands of years, and it is not surprising that we found them to have a slight tendency towards diurnality. Previous studies have found great inter-individual differences in the temporal organization of behavior in domestic cats [38].

Although the Pampas cat exhibited a slight tendency towards diurnality in our study, this species has been described as nocturnal in high-altitude deserts of the Andes [58]. The discrepancy may be related to the large difference in habitat characteristics between sites but is most likely due to differences in the quantification of diurnality. As indicated above, we found a wide gradient of diurnality in the nine felid species that we studied, with only the margay being strongly nocturnal and the jaguarundi being strongly diurnal. Also, our study involved a single specimen of Pampas cat, which may or may not be representative of the whole species.

One limitation of our study is that we did not have a large enough number of individuals of each species to conduct a comparison of rhythmic parameters between males and females or between individuals of different ages. However, by studying the temporal organization of behavior of adult individuals under controlled conditions, we gained knowledge about the “spontaneous” pattern of daily activity that can be observed in the absence of marked variations in ambient temperature, prey availability, predation risk, and other variables that confound the role of the light-dark cycle in the modulation of circadian rhythms.

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Table 1. The nine species used in the study.

Common name	Latin name	BM (kg)	Sample size	Study site	Living space (m)
Margay	*Leopardus wiedii*	4	6 (4 M, 2 F)	Foz do Iguaçu, Brazil	2 x 5 x 5
Domestic cat	*Felis catus*	4	6 M	Santa Fe, Argentina	1 x 2 x 1
Pampas cat	*Leopardus colocolo*	4	1 M	Santa Fe, Argentina	2 x 1 x 1.5
Oncilla	*Leopardus tigrinus* *Leopardus guttulus*	4	6 (3M, 3F)	Candelaria, Argentina	3 x 3 x 3
Geoffroy's cat	*Leopardus geoffroyi*	5	8 M	Santa Fe, Argentina	3 x 3 x 3
Jaguarundi	*Puma yagouaroundi*	5	4 (2 M, 2 F)	Puerto Iguazú, Argentina	4 x 10 x 5
Ocelot	*Leopardus pardalis*	7	6 M	Santa Fe, Argentina	6 x 4 x 4
Puma	*Puma concolor*	31	8 M	Santa Fe, Argentina	10 x 6 x 5
Jaguar	*Panthera onca*	75	1 M	Candelaria, Argentina	50 x 40 x 6

Fig. 1. Historical and current geographical distribution of South American felids in Argentina. The yellow dot indicates the location of the research facilities for each species. Adapted from https://felinosdeargentina.com.ar.

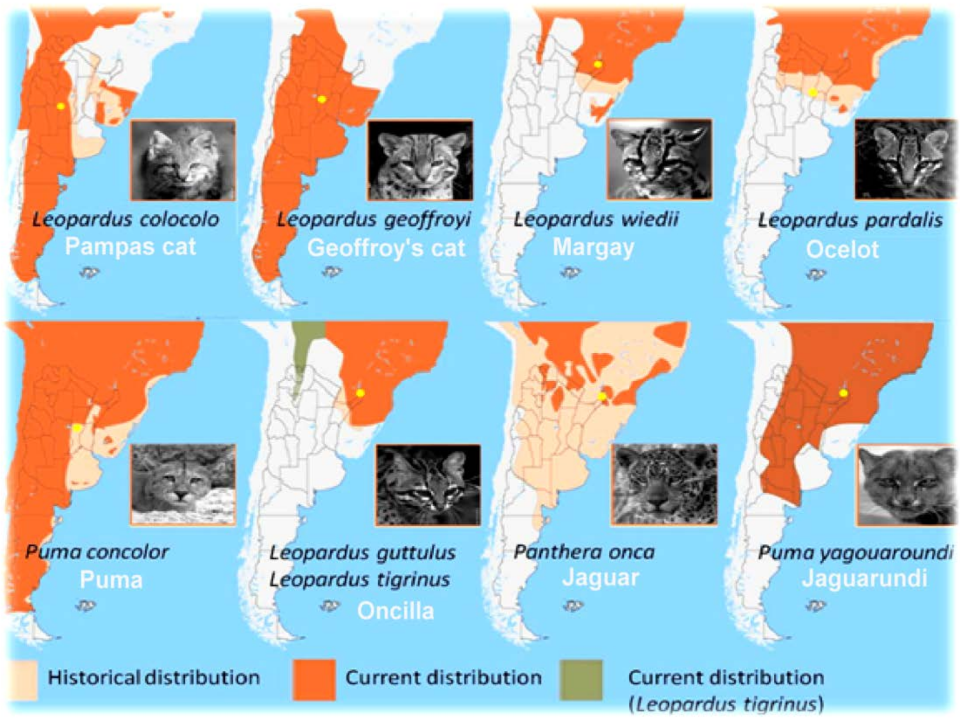

Fig. 2. Facility in which the jaguar was housed during the study. The animal can be seen lying on the wooden structure in the center of the photograph.

Fig. 3. Nine-day record of activity of a representative Geoffroy's cat. The horizontal light and dark bars above the graph indicate the duration of the light and dark phases of the light-dark cycle, respectively.

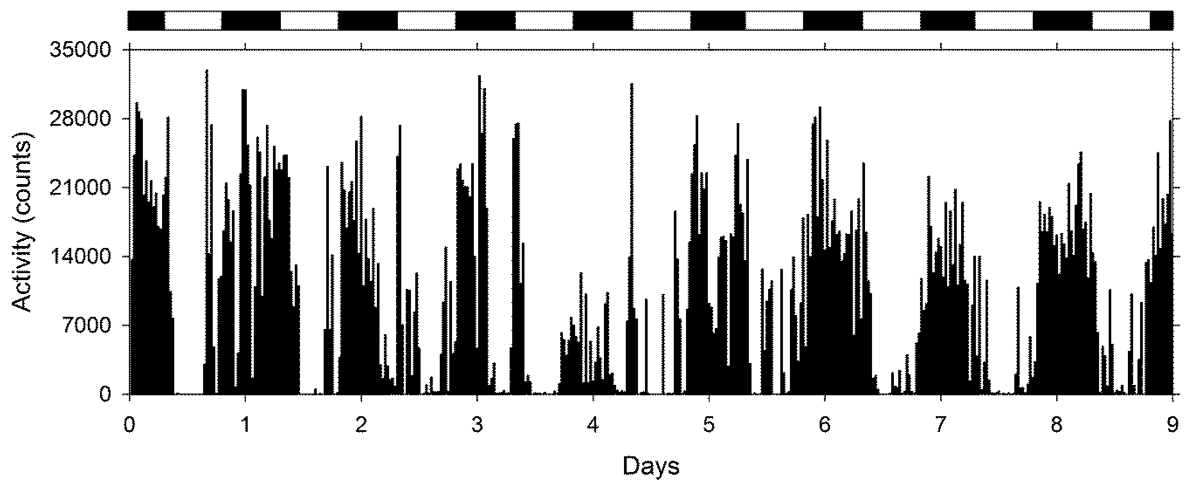

Fig. 4. Average daily pattern (wave form) of activity of the nine felid species. Each point was computed as the average of 13 days for each individual and then the average of each time of day for all the individuals of that species. The error bars are the standard errors of the overall means. The horizontal light and dark bars above the graphs indicate the duration of the light and dark phases of the light-dark cycle.

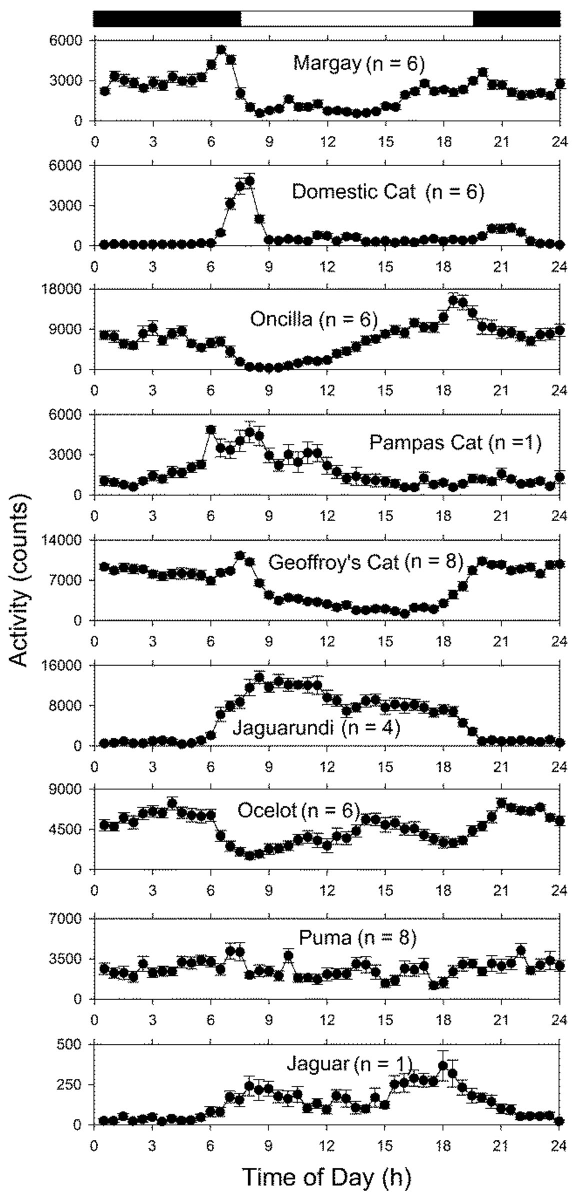

Fig. 5. Means (±SEM) of the acrophases (A), robustness (B), and diurnality (C) of the activity rhythms of the nine felid species. In each panel, bars with the same letter (a, b, c, d, or e) are not significantly different from each other, as determined by *post hoc* comparisons with Tukey's HSD test. The gray areas in the top panel denote the dark phase of the light-dark cycle.