

Activity pattern of *Cuniculus paca* (Rodentia: Cuniculidae) in relation to lunar illumination and other abiotic variables in the southern Brazilian Amazon

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ABSTRACT. Understanding what influences the activity of organisms is important for both ecological understanding and species conservation. Using data from 2,707 camera trap days distributed across 24 forest sites, we present quantitative analyses of the activity pattern of *Cuniculus paca* (Linnaeus, 1766) in southern Amazonia. We compared the activity pattern of this species across four designated subsets of the 24-hours diel cycle (dawn, dusk, day and night). Using linear regression models we tested the influence of season, temperature and rainfall on the activity patterns of *C. paca* (*paca*). We also evaluated the nocturnal photos of *paca* (N = 111) as a function of the degree of lunar illumination in order to test the prediction that pacas minimize their activity during moon phase when illumination is brighter. Pacas were not recorded during the day but were active at dawn, dusk and night time. We found differences in the influence of the abiotic variables on the nocturnal activity of pacas in the study area. There was no significant difference between the observed (expressed as the frequency of total counts of independent photos over the five classes of lunar illumination) and the expected activity of pacas, based on the frequency of days in the lunar cycle with different classes of lunar illumination, whereas lunar illumination had a weak negative influence on the timing of *paca* activity (i.e. pacas were active closer to sunset with increasing lunar illumination). However, the timing of nocturnal activity in pacas was not influenced by season, temperature or rainfall. Our findings highlight the ecological plasticity of this Neotropical rodent which has a key function in the maintenance of Neotropical forests.

KEY WORDS. Behavioral flexibility; camera trapping; lunar phobia; moon phase; temporal activity.

Animal behavior changes throughout the day, thus the temporal aspect of activity is an important dimension of an individual's ecological niche, and patterns of diel behavior can directly influence individual fitness (KRONFELD-SCHOR & DAYAN 2003). Understanding what influences the timing of activity is therefore relevant to understanding how species adapt to and persist in their environments (LIMA & ZOLLNER 1996, BUCHHOLZ 2007).

The activity of mammalian species varies with a wide variety of factors including season (DONATI & BORGOGNINI-TARLI 2006), lunar luminosity (FERNANDEZ-DUQUE & ERKERT 2006, SCHWITZER *et al.* 2007, LUCHERINI *et al.* 2009), temperature (CHAPPELL 1980), competition (WASSERBERG *et al.* 2006), predation (SUNDELL *et al.* 2004, GRIFFIN *et al.* 2005, COLQUHOUN 2006, BOROWSKI & OWADOWSKA 2010), resource availability (THEUERKAUF *et al.* 2003, TARNAUD 2006, THIES *et al.* 2006, LAMBERT *et al.* 2009), habitat fragmentation (NORRIS *et al.* 2010) and anthropogenic disturbance (KITCHEN *et al.* 2000, DI BITETTI *et al.* 2008). Lability in temporal activity therefore makes mammal species optimal for investigations into the role of time in defining a species' ecological niche.

Several studies have documented the influence of moonlight on the behavior of many nocturnal mammals including rodents (KOTLER *et al.* 1993), lagomorphs (GILBERT & BOUTIN 1991), badgers (CRESSWELL & HARRIS 1988), bats (KARLSSON *et al.* 2002), and primates (GURSKY 2003). "Lunar phobia", where nocturnal species avoid bright moonlight, has been frequently documented. This avoidance can be expressed in different behaviors, such as: reducing the use of open areas (GILBERT & BOUTIN 1991, KOTLER *et al.* 1993), restricting foraging activity (CRESSWELL & HARRIS 1988, KOTLER *et al.* 1993), and/or reducing the duration of an activity (KOTLER *et al.* 1993). Studies have also demonstrated "lunar philia" in nocturnal species (KARLSSON *et al.* 2002, GURSKY 2003) and several hypotheses for the adaptive benefits of increased activity during moonlit nights have been proposed, including: 1) the increased foraging efficiency outweighs increased predation risk during full moons, and 2) predation risk is not greater during full moons (GURSKY 2003). However descriptions of/and explanations for lunar phobia and lunar philia in wildlife species remain scarce.

Behavioral studies that attempt to untangle the ecological relevance of species behavior in general and activity pat-

terns in particular are often limited by difficulties of investigating wild populations, particularly for mammals, which are often both cryptic and capable of flexible behavioral patterns (SUNDELL *et al.* 2004). Indeed, the challenges of studying cryptic species is one of the reasons why even the most basic natural history data is lacking for the majority of Neotropical mammals (COSTA *et al.* 2005). The application of techniques which remotely monitor species can overcome some of the difficulties facing behavioral studies of wild populations and reveal unknown or poorly documented behavior in situations where direct observation is not logistically or financially possible (ALTMANN & ALTMANN 2003).

Despite the importance of *Cuniculus paca* (Linnaeus, 1766) in the dynamics of Neotropical forests (BECK-KING *et al.* 1999, DUBOST & HENRY 2006), relatively little attention has been given to investigating the activity of this ubiquitous rodent in detail. Through analysis of data from a 19 month camera trapping campaign in southern Amazonia, we ascertained how lunar illumination and other abiotic factors affect *C. paca* activity. We specifically tested the hypothesis that pacas will minimize their activity during the moon phases when illumination is brighter.

MATERIAL AND METHODS

Field surveys were carried out during 19 months (October-December 2007, January-December, 2008 and March-June 2009) within 24 forest sites, across a 4,650 km² landscape surrounding the town of Alta Floresta, state of Mato Grosso, Brazil (09°53'S, 56°02'W, Fig. 1). Deforestation in this landscape resulted from an agricultural resettlement scheme dating from the early 1980s. The Alta Floresta landscape currently consists of primary forest remnants of various sizes, shapes, and levels of structural and non-structural forest disturbance, surrounded by an open-habitat matrix dominated by cattle pastures (MICHALSKI *et al.* 2008).

The mean annual rainfall is 2,350 mm, and the evapotranspiration is ~1,000 mm/year, providing a 1,350-1,400 mm/year surplus, except for the dry season (May-September), which typically results in a hydrological deficit of 250-300 mm (RADAMBRASIL 1983). We distributed our sampling across the entire year in 2008 and in both, wet and dry seasons in 2007 and 2009, which minimized any confounding effect of rainfall seasonality.

Pacas are mid-sized (circa 9 kg) nocturnal terrestrial rodents that can be found in a variety of forest habitats, but prefer areas close to water (LEOPOLD 1959). They are predominantly solitary, with adults defending their territory against members of the same sex (EISENBERG 1989). Their diet is largely frugivorous but during periods of fruit shortage they also feed on seeds, leaves, and some tubers (EMMONS & FEER 1997, DUBOST & HENRY 2006). This rodent appears to be slightly area-sensitive (MICHALSKI & PERES 2007, NORRIS *et al.* 2008), but is often found

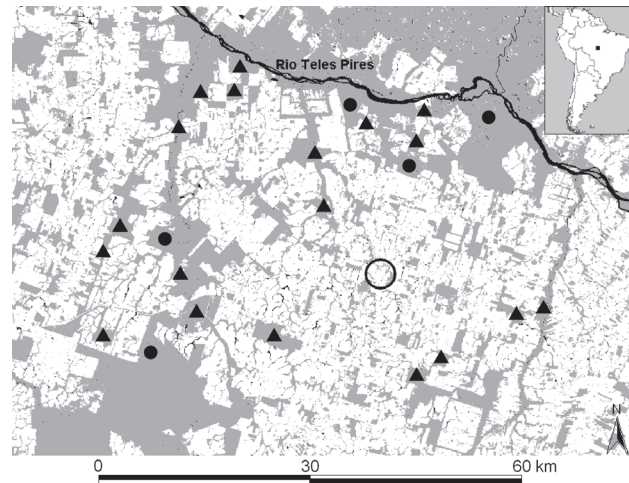


Figure 1. Location of the study area in Alta Floresta, northern Mato Grosso state, Brazil (see inset for location). A classified Landsat TM image (227/67, October 10, 2008) shows the 19 forest fragments (solid triangles) and five continuous forest sites (solid circles) surveyed by remote camera trapping in 2007-2009. The large open circle shows the location of Alta Floresta town. Grey, white and black areas represent forest, non-forest, and open-water cover, respectively.

in highly disturbed areas (NAUGHTON-TREVES *et al.* 2003), and is extensively hunted throughout its range (PEREZ 1992).

Camera traps (Tigrinus, Santa Catarina, Brazil) with infra-red motion detectors were used to continuously record the activity of the target species. Camera traps were baited with scent lure (Hawbaker's Wild Cat Lure 2; Minnesota Trapline Products, Pennock, Minnesota), and set to record date and time of all photos, working continuously over the 24-hour diel cycle. Cameras were operational for a total of 30 consecutive days within each of the 24 forest sites surveyed, including 19 forest fragments ($\geq 1,000$ ha) and five undisturbed continuous forest areas. We maximized the spatial independence between preselected sites by establishing a minimum edge-to-edge distance >1 km (mean \pm SD = 31.0 ± 14.6 , range = 3.4-63.0 km, $n = 276$ pairwise comparisons).

Within each site cameras were placed 30-40 cm above ground and checked every 3-4 days to renew the scent lure, batteries and films as necessary (NORRIS *et al.* 2010). We distributed camera traps within each fragment along perennial rivers, close to forest edge and in the core area (> 500 m from the nearest edge) with a minimum distance of 500 m, thereby ensuring a large area sampled in each forest site. All camera trap locations were under closed canopy forest which enables us to assume that the minimum variation in light penetration did not effectively influence our results. Trapping periods and effort varied among sites, with a minimum of two and a maximum of ten camera traps per site.

We were unable to identify individuals unambiguously; therefore consecutive photos of the same species in the same camera trap were defined as independent occurrences if the interval between photos was one hour or more (NORRIS *et al.* 2010).

Because we did not measure environmental variables at each camera location, qualitative indexes were derived to quantify the relative influence of nocturnal illumination, mean temperature, and total precipitation on the timing of photos (NORRIS *et al.* 2010). Data for moon phase, illuminated fraction, civil twilight (when the sun is 6° below the horizon) and moonrise and moonset were obtained from the United States Naval Observatory Calendar (<http://aa.usno.navy.mil>), using the Alta Floresta geographical coordinates (09°52'S, 56°06'W, GMT -4 h). The geographic proximity of the cameras (maximum nearest neighbor distance = 63 km) and the small altitudinal variation in the study area (200-300 m) (RADAMBRASIL 1983) means that sunset and sunrise do not vary significantly between our camera sites. Values for mean temperature (°C) and total precipitation were collected via a Stevenson weather station located at the Alta Floresta Airport (location = 09°52'S, 56°06'W, SYNOP id = 82965) and obtained from the weather monitoring centre of the Brazilian National Institute of Space Research (<http://www.cptec.inpe.br>).

To analyze activity patterns we pooled the data from all study sites. By pre-selecting forest sites > 1000 ha we controlled for the effects of forest loss and fragmentation. Previous studies have demonstrated that area effects are most apparent in forest sites < 1000 ha in the region, whereas in areas > 1000 ha there is little or no effect of forest loss and fragmentation and or anthropogenic perturbations on faunal (mid to large bodied mammals – MICHALSKI & PERES 2005, 2007, NORRIS *et al.* 2008, NORRIS *et al.* 2010) and floral communities (tree functional groups – MICHALSKI *et al.* 2007) in this recent deforestation frontier.

All analyses were conducted in the R-Software (R DEVELOPMENT CORE TEAM, 2010). Circular summaries (LUND & AGOSTINELLI 2010) were used to determine the mean overall timing of paca activity over the 24-hours period as recorded by camera traps. We adopted different analytic approaches to understand how lunar illumination and other abiotic variables influenced “if” and “when” pacas were active. Chi-squared tests (χ^2) were used to quantify “if” the frequency of paca activity during the 24-hours diel period and on nights with different lunar illumination differed from expected. Linear regression models were used to examine whether lunar illumination and other abiotic variables explained “when” pacas were active during the 24 diel and nocturnal periods.

We also used Chi-squared to investigate if the activity of pacas differed from expected with respect to time of day by grouping the photos obtained into four time periods: day (one hour after sunrise to one hour before sunset), night (one hour after sunset to one hour before sunrise), dawn (from one hour before to one hour after sunrise), and dusk (from one hour before to one hour after sunset) (THEUERKAUF *et al.* 2003). Expected values

were obtained from the proportion of hours in the 24-hour cycle corresponding to each of the four diel classes.

Chi-squared tests were also used to explore the effect of the lunar cycle on the frequency of paca activity i.e. “if” pacas were active on any particular night. Two sets of frequency counts from I) all nocturnal photos and II) “moon photos” (nocturnal photos taken when the illuminated fraction of the moon was apparent in the night sky) were obtained for five lunar classes (LUCCHERINI *et al.* 2009): moonless (moon not present) and four categories of increasing brightness, defined by the percentage of illuminated moon (1-25%, 26-50%, 51-75%, and 76-100%) visible at midnight in Alta Floresta (as described in NORRIS *et al.* 2010). We compared the observed frequency counts over the five lunar classes with those expected based on the proportion of days in the 29.5 day lunar cycle with illumination values corresponding to the brightness classes.

We used a linear scale to quantify “when” pacas were active – with the response defined as the difference in time (hours) of the photo from sunset (civil twilight). We used linear regression models to examine whether this response was explained by abiotic variables (season, average daily temperature, total daily rainfall, and lunar illumination). We carried out separate regression models to understand how these variables explained when paca were active over both diel (all photos recorded) and nocturnal (from one hour after civil twilight to one hour before civil sunrise) periods. We adopted a backwards stepwise selection (R function “step”) applying the program defaults to arrive at a most parsimonious (“best”) model. We compared variable slope and standard error estimates in both the full and the “best” model selected, which enables us to avoid well known issues of stepwise approaches e.g., inflated Type 1 error rates (MUNDRY & NUNN 2009). We preferred this selection approach to alternatives such as Information Theoretic model averaging (as applied in NORRIS *et al.* 2010) as we consider it more than appropriate to yield useful explanatory insight (MURTAUGH 2009) based on the data available and our study objectives.

RESULTS

We obtained 128 (0.05 photos/trap day) independent photographs of pacas during 2,707 camera-trap days in our study region. From this total, 111 and 36 photos were nocturnal and “moon photos” (i.e., nocturnal photos taken when the illuminated fraction of the moon was apparent in the night sky), respectively.

Diel activity

We found a significant difference from the expected frequency of photos across the four diel periods (χ^2_3 , 122.24, $p < 0.0001$). This pattern resulted from the predominantly nocturnal activity of pacas, with 86.7% of all photos recorded during the night (Fig. 2) and 100% of records registered between an hour before sunset and sunrise on the following day (Fig. 2).

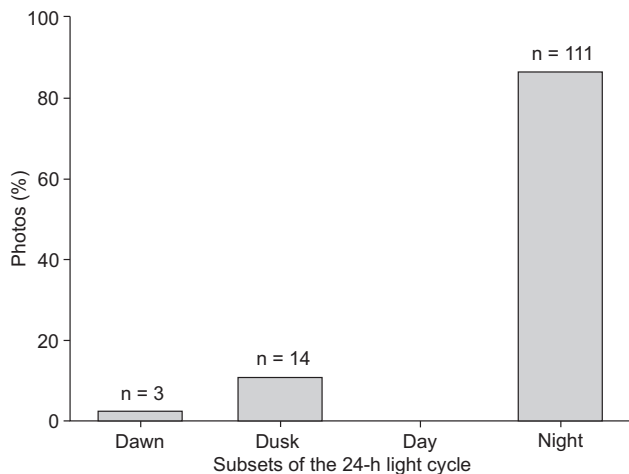


Figure 2. Activity patterns for *Cuniculus paca* as determined from camera trapping in southern Amazonia. The sample size of photos obtained is noted above each column. Data represent the percentage of photos occurring within each of 4 designated subsets of the 24-hours diel cycle.

Circular means obtained from the time of photos showed that on average pacas were active at 22:32 h, approximately 4.5 hours after sunset. Although pacas had a narrow period of activity (Fig. 3) considering the full 24-hours cycle, photos were recorded between 18:00 h and 04:00 h, overlapping dawn and dusk, which indicates that pacas have a broad range of activity throughout the night.

Linear regression models revealed that lunar illumination influenced the timing of diel activity in pacas (Tab. I). Although statistically significant, our most parsimonious models showed lunar illumination did not provide a substantial contribution towards explaining the variation in the timing of diel activity for pacas ($R^2_{Adj} = 0.026$).

Nocturnal activity

The highest peak of activity from all nocturnal photos of pacas occurred when the degree of lunar illumination was 1-

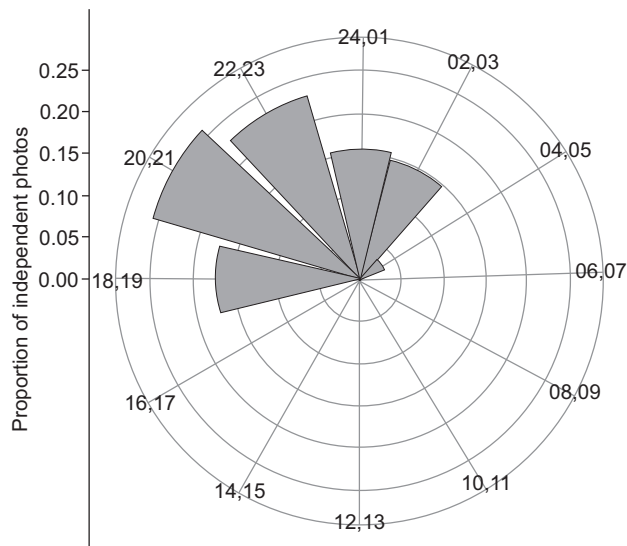


Figure 3. Proportion of independent *Cuniculus paca* photos recorded over a 24-hour cycle presented in 2-hour bins (e.g., "22, 23" includes all photos between 22:00:00 and 23:59:59 h) obtained with camera traps in 19 forest fragments and five undisturbed areas of continuous forest sites surrounding the town of Alta Floresta, Mato Grosso, Brazil.

25% (Fig. 4), whereas 50% of "moon photos" were recorded during the brightest class of lunar illumination (76-100%, Fig. 4). However, the observed paca activity (expressed as the frequency in total counts of independent photos over the five classes of lunar illumination) did not differ from the expected based on the frequency of days in the lunar cycle with the different classes of lunar illumination ($\chi^2_4, 5.379; p = 0.251$, $\chi^2_4, 6.184; p = 0.186$, all and "moon photos", respectively).

Although the χ^2 test showed that the degree of lunar illumination did not influence if pacas were active on a particular night, our regression analysis revealed that lunar illumination did influence when pacas were active during the night (Tab. I). The most parsimonious model revealed that lunar illumina-

Table I. Slope coefficients (\pm SE) from linear models with predictors of the timing of *Cuniculus paca* activity (24 h – "All photos", nocturnal – "Nocturnal photos") monitored with camera traps in 24 forest sites surrounding the town of Alta Floresta.

Model components	All photos		Nocturnal photos	
	Complete	Best ^b	Complete	Best ^b
Season ^a	-0.163 (0.168)	–	-0.012 (0.076)	–
Average temp	-0.015 (0.022)	–	-0.009 (0.009)	–
Total rainfall	0.000 (0.006)	–	0.001 (0.003)	–
Lunar illumination	†-0.443 (0.242)	*-0.497 (0.234)	*-0.237 (0.114)	*-0.241 (0.110)
	$F_{4,123} = 1.44, R^2_{Adj} = 0.013$	$*F_{1,126} = 4.33, R^2_{Adj} = 0.026$	$F_{4,106} = 1.55, R^2_{Adj} = 0.020$	$*F_{1,109} = 4.84, R^2_{Adj} = 0.034$

Significance levels: † < 0.1, * < 0.05, ** < 0.01, *** < 0.001; ^aSlope estimates for season are based on the comparison of wet with dry season; ^b The most parsimonious model obtained from backwards model selection based on comparison of AIC values.

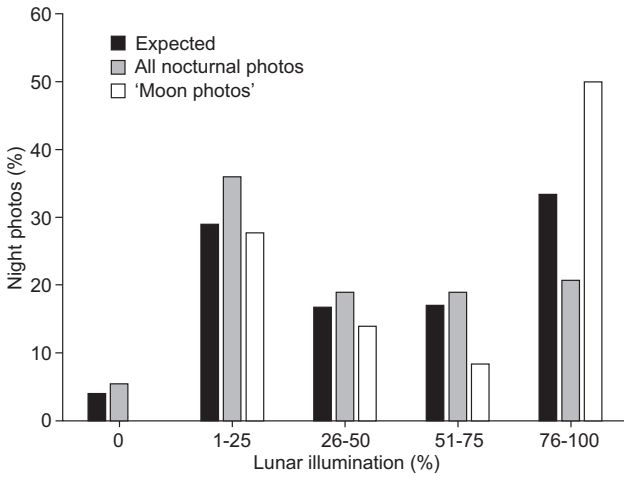


Figure 4. Distribution of photos of *Cuniculus paca* as a function of degree of lunar illumination. Expected proportion of photos, all nocturnal photos ($n = 111$), and 'moon photos' ($n = 36$) are shown.

tion had a weak ($R^2_{Adj} = 0.034$) negative influence on the timing of pacas activity (i.e. pacas were active closer to sunset with increasing lunar illumination), whereas season, temperature or rainfall exerted no influence on the timing of nocturnal activity in pacas.

DISCUSSION

Contrary to what we had predicted, pacas did not minimize their activity during the moon phases with brighter illumination. This finding suggests that other variables may influence *C. paca* activity and/or that the activity of pacas within nocturnal periods is flexible, enabling them to adapt to different abiotic conditions.

By evaluating the responses in diel and nocturnal activity of pacas in the Brazilian Amazon to abiotic variables such as degree of lunar illumination, we have provided insights for the ecology and conservation of the species. Through the breakdown of temporal activity from coarse scale to hourly periods we have also demonstrated the importance of considering the temporal scale in understanding species responses over the 24 hours diel cycle.

Diel and nocturnal activity patterns

The diel periods of activity we found for pacas generally agree with previous studies which have shown that the species is predominantly nocturnal (EMMONS *et al.* 1989, PEREZ 1992, HARMSSEN *et al.* 2011).

Previous authors have reported that *C. paca* is "lunar phobic" and that the lunar cycle and/or lunar illumination strongly influences the activity of individuals (EMMONS *et al.* 1989, PEREZ 1992, HARMSSEN *et al.* 2011). Lunar phobia in nocturnal mammals can be explained by one of two strong selective

pressures: predation risk or prey availability (BORK 2006, LANG *et al.* 2006). Previous studies have explained lunar phobia in *C. paca* as an anti-predator response (HARMSSEN *et al.* 2011). However, we have found that pacas activity (measured as the frequency of photos per lunar illumination class) did not differ significantly with lunar illumination (i.e. we were unable to detect any significant influence of lunar illumination on "if" pacas were active during a particular night).

A possible explanation for the difference in pacas activity between studies comes from the findings of EMMONS *et al.* (1989) that pacas avoid open areas during moonlit nights. HARMSSEN *et al.* (2011) surveyed secondary forest areas with cameras mostly positioned on open (i.e. greater than one meter wide) trails or roads (HARMSSEN *et al.* 2010, HARMSSEN *et al.* 2011) whereas our cameras were located in primary forest areas away from open trails. Therefore, the results of HARMSSEN *et al.* (2011), showing less active pacas under more intense lunar illumination, could be an artifact created by the secondary forest habitat where they carried out their studies. Secondary forests (20-100 years old) are known to have lower, less complete canopies and a greater number of small canopy gaps (GUARIGUATA & OSTERTAG 2001, PENA-CLAROS 2003). These small canopy gaps enable increased levels of lunar illumination to reach the forest floor when compared to primary forest areas such as those surveyed in the present study, which have a dense overstory. In our study area, the dense canopy effectively limits the amount of lunar illumination reaching the forest floor even on the brightest nights.

In our southern Amazonian forest sites lunar illumination was the only variable that (weakly) explained variation in the timing (expressed as time after sunset) of diel (24 hours) and nocturnal activity for pacas. Our regression analysis revealed that neither of the other abiotic variables investigated (rainfall and temperature), nor illumination, provided any convincing explanation of the variation in the patterns of "when" pacas were active.

Unexplained variation in temporal activity

Nocturnal activity in mammals is facilitated by physiological adaptations (CROMPTON *et al.* 1978, HEESY & HALL 2010). Pacas have a specialized vision including the *tapetum lucidum* (SILVEIRA *et al.* 1989), an intraocular reflecting structure that increases retinal sensitivity (OLLIVIER *et al.* 2004). Besides the *tapetum lucidum*, pacas also have retinal ganglion cells, which have been shown to integrate information from wider areas of the visual spectrum compared with diurnal species such as agoutis – *Dasyprocta* spp. (SILVEIRA *et al.* 1989). These ganglion cells are thought to be an adaptive advantage that facilitates the processing of visual information at low light levels (HUGHES 1977). Therefore, the predominance of nocturnal activity in pacas is to a large extent "hard-wired" by evolutionary constraints.

Within the limits imposed by evolutionary constraints, pacas exhibit variation in activity that is not directly explained by lunar illumination or other abiotic factors. The unexplained

variation in temporal activity of pacas found in our study area may be caused by variations in unmeasured covariates such as habitat structure and predation risk. Although large felids such as *Panthera onca* (Linnaeus, 1758), and *Puma concolor* (Linnaeus, 1771), the main predators of pacas (NOVACK *et al.* 2005), do occur in the study area (MICHALSKI *et al.* 2011), and despite the fact that the forest fragments studied are all large enough to encompass the entire vertebrate assemblage (MICHALSKI & PERES 2007), we believe that the study region has a lower overall density of large predators when compared with that of other studies (e.g., HARMSSEN *et al.* 2011), due to its fragmented landscape. In fact, human-wildlife conflicts across our study region are responsible for a relatively high annual mortality of large felids (MICHALSKI *et al.* 2006). As a consequence, Neotropical rodents such as pacas may be adopting a more flexible behavior, with reduced predator densities “releasing” them from the limiting effects of predation risk. Therefore, reduced predation risk enables pacas to be active across the entire lunar cycle, without the need to avoid strongly illuminated nights.

ACKNOWLEDGEMENTS

FM was funded by a Fundação de Amparo à Pesquisa do Estado de São Paulo Pos-doc scholarship (FAPESP 2007/01252-2). This study was funded by the Wildlife Conservation Society, Conservation, Food and Health Foundation, Cleveland Metroparks Zoo and the Cleveland Zoological Society and the Rufford Small Grants Foundation. We thank the national Centre of Research and Conservation of Carnivores (CENAP/ICMbio) for logistical support. We are deeply indebted to the landowners who contributed to this study and especially to Geraldo C. Araújo and Alex G. Araújo.

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Submitted: 27.VIII.2011; Accepted: 16.XI.2011.

Editorial responsibility: Kleber Del Claro