



Original investigation

Phylogenetic signal in the circadian rhythm of morphologically convergent species of Neotropical deer

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ABSTRACT

Deer species included in the genus *Mazama* descend from two different clades that experienced a strong evolutionary convergence in morphology and behaviour when they adapted to Neotropical forests. We would expect that circadian activity rhythms also converged according to habitat features or responded to temporal niche segregation in sympatric species. We used camera trapping in four study areas, representing three main biomes in Brazil, together with data taken from the literature, to analyse activity patterns of five *Mazama* species in four biomes in South America. Our results show that clade assignment was the main predictor of diurnal versus nocturnal activity, thus suggesting a phylogenetic constraint rather than any other ecological influence on circadian activity. We discuss how the evolutionary history of both lineages may have influenced their activity patterns.

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Introduction

Flexibility is a widespread property of many behavioural traits (Piersma and Drent, 2003; Foster and Sih, 2013). Plasticity in circadian activity patterns may allow species to cope with variations in conditions between areas and seasons (Kammermeyer and Marchinton, 1977; Beier and Mccullough, 1990; Webb et al., 2010; Owen-Smith and Goodall, 2014) or to coexist with minimal disturbance (Monterosso et al., 2014). On the other hand, the circadian rhythm is a deep phylogenetic feature for many taxa (Kronfeld-Schor and Dayan, 2008; Roll et al., 2006). This is because physical oscillations like the day/night dichotomy are among the most predictable environmental cues that animals perceive, such that selection has favoured the development of internal mecha-

nisms, like the circadian clock, associated with activity rhythms that rely on these cycles (Kronfeld-Schor and Dayan, 2003). Synchrony with the day/night cycle has become an important source of selection for morphological and physiological adaptations that affect many life history traits and allows for temporal niche axis partitioning (Kronfeld-Schor et al., 2001). All these specialisations affect numerous traits, including the predominant use of particular senses like vision versus smell and hearing, either for locating food, for intraspecific communication or for detecting predators, and for the development of colour patterns for camouflage or for aposematic signalling. The likely consequence of the majority of these adaptations is that the efficiency of activity at other times will be strongly reduced (Jacobs, 1993; Van Schaik and Griffiths, 1996), and hence they constrain the maintenance of real flexibility in activity patterns.

There are examples in the literature where activity patterns appear flexible (e.g. African ungulates: Owen-Smith and Goodall, 2014; fishes: Fox and Bellwood, 2011) or seem to be constrained by

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phylogeny (e.g. rodents: Roll et al., 2006). Sister species adapted to different conditions may experience selection for different activity patterns. Likewise, convergent evolution may drive species from different taxa to acquire similar circadian rhythms. However, we still have little understanding of the ecological forces driving the evolution of activity patterns or how evolutionary processes that affect other adaptations, such as feeding habits and habitat use, also affect circadian patterns. It is thus unclear whether species from different lineages that experience evolutionary convergence after adaptation to similar environments and life styles also converge in their circadian activity rhythms.

Neotropical brocket deer included in the genus *Mazama* have been shown to constitute a polyphyletic group belonging to distant cervid lineages that adapted to forested habitats along the Neotropical Ecozone (Duarte et al., 2008; Duarte and González, 2010; Merino and Rossi, 2010). All of them show spiked antlers in males and very similar body size and shape. Five of these *Mazama* species occur in Brazil (*M. americana* [Erxleben 1777], *M. nana* [Hensel 1872], *M. bororo* [Duarte 1996], *M. gouazoubira* [Fischer 1814] and *M. nemorivaga* [Cuvier 1817]) and show strong morphological convergence (Fig. 1) despite their evolutionary origin from two different clades: the red clade, which includes *M. americana*, *M. nana* and *M. bororo*, and the grey clade, which includes *M. gouazoubira* and *M. nemorivaga* (Duarte et al., 2008). Although all these species have presumably adapted to forested areas during their evolutionary history, since they crossed the Isthmus of Panama 2.5 million years ago, each species currently occur in areas and habitats with somewhat different features (Duarte et al., 2008). *Mazama americana* is widely distributed through most forests of South America from Colombia to Northern Argentina (Varela et al., 2010). *Mazama nana* is associated with the mixed ombrophilous forest in southern Brazil and part of Paraguay and Argentina (Abril et al., 2010), while *M. bororo* is found in a restricted area of the southern Brazilian coast where dense ombrophilous forest occurs (Vogliotti and Duarte, 2010). *Mazama gouazoubira* is associated with the forested areas of the Brazilian Cerrado, but can also occur in more open lands such as the Pantanal, while its clade mate *M. nemorivaga* is distributed throughout the Amazon Forest (Black-Décima et al., 2010; Rossi et al., 2010). All these habitats show differing features: dominant vegetation, types of food, main predators or human disturbances. Although detailed information on these potential differences between habitats is scarce, the effect of the habitat component on activity patterns is to be expected.

Mazama species are among the least studied species of deer (Weber and González, 2003) with scarce information about their diets or fine-scale habitat use. Their solitary habits and elusive life styles, inhabiting dense tropical forests, make it extremely difficult to observe their behaviour in the wild. However, morphologically convergent species of the *Mazama* complex provide an excellent opportunity to test the influence of phylogenetic constraints and recent ecological adaptations on activity patterns. Previous studies in the Bolivian Chaco and Peruvian Amazon found that the habits of *M. americana* (red clade) were more nocturnal than *M. gouazoubira* (grey clade) (Maffei et al., 2002; Rivero et al., 2004; Gómez et al., 2005; Tobler et al., 2009). No information is yet available for other species within both clades and for other habitats where they occur in their distribution ranges.

In this research, we used camera traps placed at different locations throughout Brazil to study the circadian activity rhythm of five brocket deer species that belong to two different clades and show strong morphological and life style convergent features, but currently inhabit different habitats. We also used published information on *Mazama* species at other sites in South America, together with our own data, to test the influence of habitat types and phylogenetic relationships on activity patterns. The main

hypotheses to be tested, i.e. possible outcomes of our comparison, were (i) similar circadian patterns for all species, probably indicating a convergence process matching morphology and life style, (ii) differences between circadian rhythm related to the different habitats they inhabit, suggesting adaptations to ecological conditions and (iii) activity patterns related to the phylogenetic clades they belong to, which could reveal a phylogenetic constraint.

Material and methods

Study areas and sampling

Our sampling was based on camera traps that were set to work 24 h each day and positioned in places that deer are known to use and where they pass, such as paths, muddy soil sites and small streams. The camera traps registered the date and time of each photo. We conducted the surveys with camera traps in four areas in Brazil: Iguaçú National Park and Intervales State Park in the Atlantic Forest; Jamari National Forest in the Amazon Forest; and Nhimirim Farm in the Pantanal, encompassing 3 different biomes and a broad latitude range from 9° to 25° South (Fig. 2). In addition to our own fieldwork, we reviewed published papers and found four studies that used camera trapping to study activity rhythms for *Mazama* species in different habitats in South America: Rivero et al. (2005), Gómez et al. (2005), Di-Bitetti et al. (2008) and Tobler et al. (2009). From these papers, we extracted data on the frequency of camera shots every 2 h and incorporated them into our analyses. This contributed by adding one biome to those we studied (Chiquitano forest, a type of dry Chaco forest where *M. americana* occurs in sympatry with *M. gouazoubira*), together with further information for some species at new sites within the biomes that we sampled (*M. americana* in the Bolivian Amazon, *M. gouazoubira* and *M. americana* in the Peruvian Amazon, and *M. americana* and *M. nana* in the Misiones Atlantic Forest in Argentina). See Table 1 for information on study areas and sampling effort.

Data analysis

Each photo was considered a record of species activity and all of them integrated a data file with species, sampling area, camera site, date, time and period of the day (day, night, dusk and dawn). Since the period of the day is concerned with daylight intensity, we arbitrarily classified the records by assuming that dusk and dawn are respectively one hour before and after sunrise and sunset. As this varies according to latitude and season, we classified the photos based on the time of detection and the sunrise and sunset times estimated for the specific day and place using an astronomical formula (Boczek, 1988).

Since we are working with morphological convergent species, identification was done by recognising key features that separate them (Duarte and González, 2010) and registers that were not clear were discarded. To ensure the independence of photos taken at the same camera site, we excluded from the analyses all those registers of the same species taken within an interval of less than one hour.

To describe our results on circadian rhythms for the species sampled in different habitats in Brazil, we conducted kernel density analyses for circular data (Ridout and Linkie, 2009; Oliveira-Santos et al., 2013). This analysis was performed using 6 as the smoothing parameter (k), chosen from graphical analysis of all species' activity range estimated with isopleths of 0.5 and 0.95 against a smoothing parameter ranging from 0 to 10. The smoothing parameter selected was the smallest k value for which the activity range estimation was stabilised. We also calculated the activity overlap (isopleth

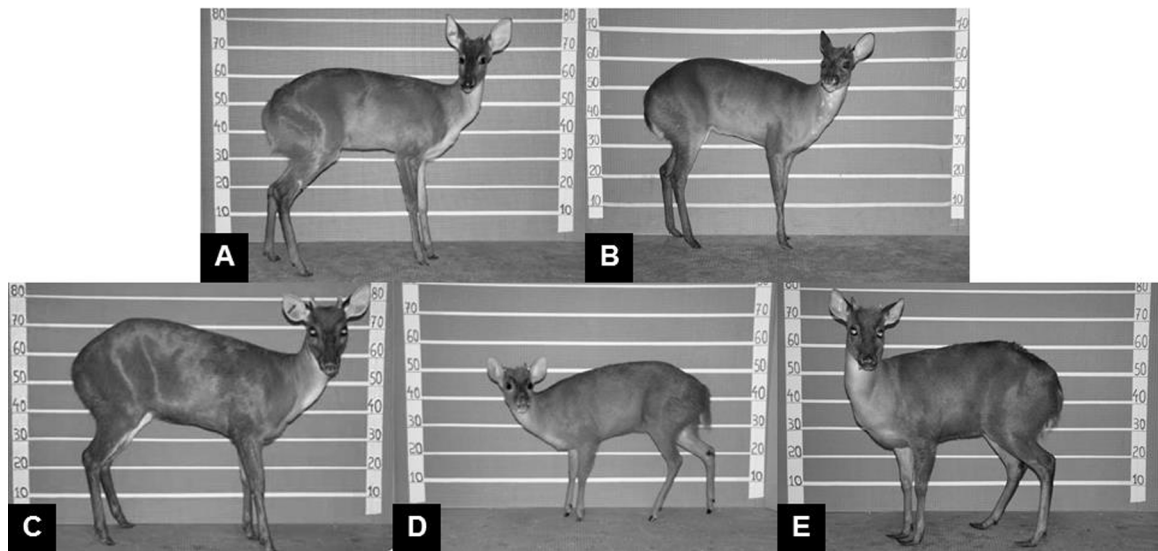


Fig. 1. Pictures of male captive specimens of the *Mazama* species that occur in Brazil, to show their high level of morphological similarities. (A) *M. gouazoubira*; (B) *M. nemorivaga*; (C) *M. americana*; (D) *M. nana*; (E) *M. bororo*. The deer belong to the Deer Research and Conservation Centre (NUPECE; Jaboticabal, Brazil) and were not used in this study, which is based on wild individuals recorded by camera trapping.

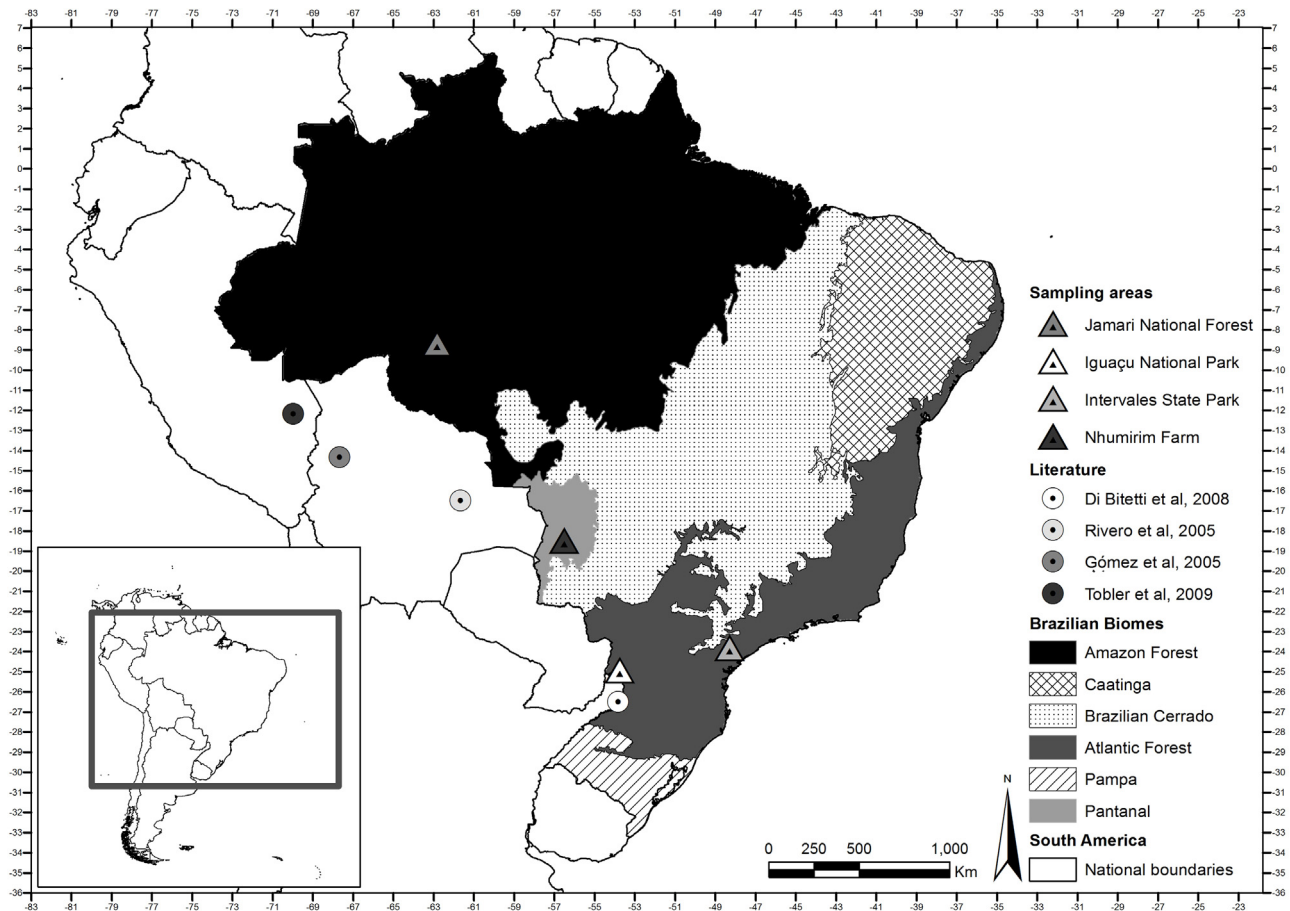


Fig. 2. Geographical location of sampling areas with respect to Brazilian biomes.

0.5) between the grey and red clades, the sympatric *M. americana* and *M. nana* in the Atlantic Forest and *M. americana* and *M. nemorivaga* in the Amazon. Both kernel and overlap analyses were performed using the R package ‘circular’ (Agostinelli and Lund, 2013).

To ensure the independence of cases used in the analyses, we grouped camera sites into areas. Cameras were placed at least 400 m from each other in the area with lower distance (Nhumirim Farm in Pantanal) but normally they were placed at >1 km distance. But even so, using each camera site as an independent case

Table 1
Detailed sampling description for different areas of our study and for the studies we collected the data from literature.

| Area | Biome | Stations (n) | Camera trap trade mark | Sampling effort (camera trap days) | Period | Source |
|-------------------------------------|-----------------|--------------|-------------------------------------|------------------------------------|---------------------|--------------------------|
| Iguaçu National Park | Atlantic Forest | 35 | Tigrinus and CamTrakker | 4018 | 2006/2008 | Our data |
| Nhumirim Farm | Pantanal | 20 | Tigrinus | 4361 | 2011–2012 | Our data |
| Intervalles State Park | Atlantic Forest | 12 | CamTrakker | 5259 | 2002–2004 | Our data |
| Jamari National Forest | Amazon | 31 | Tigrinus and CamTrakker | 3902 | 2006–2007/2011–2013 | Our data |
| Green corridor of Misiones province | Atlantic Forest | 158 | CamTrakker, TrailMAC and Leaf River | 10244 | 2003–2006 | Di-Bitetti et al. (2008) |
| Estancia San Miguelito | Chaco | 28 | CamTrakker and Trailmaster | 1695 | 2002 | Rivero et al. (2005) |
| Madidi National Park | Amazon | – | CamTrakker and Trailmaster | 3161 | 2001–2003 | Gómez et al. (2005) |
| Madre de Dios department | Amazon | 147 | Deercam and Cuddeback | 8820 | 2005–2007 | Tobler et al. (2009) |

faced at least two problems: (i) the low number of photos in some sites and also (ii) a rather low confidence of full independence (i.e. different individuals) between some sites. Therefore, we decided to group camera sites into areas to get (i) higher sample size to characterize each case (number of photos), and (ii) full confidence of independence between cases. Within each area, we may have several individuals (we normally do not know the number) but we are quite confident that individuals using one area are different to those using other area. Thus, the pooled photos from each area constituted each independent case used in the analyses. Apart from geographical distance we also used time (i.e. different years) to define independent sampling events (see below) Thus, species data were split into two groups according to time in the Jamari National Forest (years separated by years with no sampling) and Intervalles State Park (two consecutive years), and according to space at the Nhimirim Farm (two areas of ca. 1000 ha each) and in the Iguaçu National Park (two areas ca. 60 km apart). Thus a total of 20 cases (11 from our own sampling and 9 from the literature) were included in the analyses representing species at independent sampling events/sites.

To investigate the association between factors like habitats or phylogenetic clades and the activity patterns, we conducted two type of analyses. On one hand, cluster analysis (complete linkage with Chebyshev distance) was used to group activity patterns according to habitats or clades. We included both for our own data from fieldwork and those from the literature. For this analysis, we used the percentage of independent photos taken distributed every two hours (hence 12 intervals per day). This analysis was performed using BioEstat 5.3 software (Ayres et al., 2007).

On the other hand, we conducted a Linear Mixed Model to investigate the relative effect of habitats and phylogenetic groups to predict the proportion of diurnal activity as the dependent variable. Activity records were aggregated into diurnal (day and dawn due to the strong correlation between them, see below) and nocturnal (dusk and night, also strongly correlated). In addition to our own data, we extracted the percentage of diurnal records for each species in the different environments from the published papers mentioned before, and included them in our Linear Mixed Models. The dependent variable was the proportion of diurnal detections (Diurnal). Normality of the response variable was assessed by inspecting Q–Q plots and by the Kolmogorov–Smirnov normality test. Before applying the linear regression, we transformed the dependent variable by using the logit link function, as this is a commonly used transformation in cases in which the dependent variable has values that fall between 0 and 1. Residuals from models with the transformed variable showed a clear improvement in achieving the linear models' criteria. Random subjects were sampling events (study areas and years, see above) for each species, and fixed factors were species, clade (red and grey) and habitat (Amazon Forest, Atlantic Forest, Chaco and Pantanal). We conducted two models, one for factors clade

and habitat and another one for species and habitat. One of the cases of *M. americana* in Atlantic Forest was removed from the models because it appeared as a clear outlier in the residual plots, although the main results did not change by including it. Linear Mixed Models were performed in SPSS v.20 (SPSS, Chicago, IL, U.S.A.). Since variable transformation makes difficult the interpretation of parameter estimates, we represented in figures the observed non-transformed values (expressed as percentages).

Results

We obtained a total of 1347 independent records for all sampling areas, 493 of *M. gouazoubira* at the Nhimirim Farm (Pantanal), 64 of *M. americana* and 59 of *M. nemorivaga* in the Jamari National Forest (Amazon Forest), 383 of *M. bororo* in the Intervalles State Park (Atlantic Forest), 259 of *M. americana* and 89 of *M. nana* in the Iguaçu National Park (Atlantic Forest).

The circular kernel analysis results are shown in Fig. 3. Species in all sampling areas, except *M. americana* in the Amazon Forest, presented a circadian rhythm with two close peaks of activity (isopleth 0.5). The red clade species showed a more nocturnal pattern, with *M. americana* showing some activity in the early morning in the Amazon Forest. In contrast, the grey clade species presented a concentration of activity during daylight, with *M. nemorivaga* activity occurring more clearly confined to late morning and *M. gouazoubira* more active in the early morning and late afternoon. The activity overlap between the two clades was almost null (0.001) and quite low (0.109) between the sympatric and non-phylogenetically related Amazonian species *M. americana* and *M. nemorivaga* (Fig. 4). The opposite was true for the sympatric Atlantic Forest species *M. americana* and *M. nana*, which are from the same clade and showed high overlap (0.671).

Cluster analysis (Fig. 5) split the species into two major groups that coincide with the two phylogenetic clades, while the environments (biomes) did not match this major subdivision. The number of camera shots in the four activity periods showed strong correlations between dawn and daylight on the one hand ($r=0.959$, $N=11$, $p<0.0001$) and dusk and night on the other ($r=0.958$, $N=11$, $p<0.0001$), while other relationships between periods were not significant. Therefore, we pooled the data from dawn and daylight to depict diurnal activity against dusk and night as nocturnal. Fig. 6 shows the percentage of diurnal activity for all the species and habitats studied. The Linear Mixed Model for diurnal activity as the dependent variable showed a strong effect of clade and only a marginally significant influence of habitat types (Table 2), and the results were very similar when the five species, instead of the two clades, were included as the independent factor (Table 3).

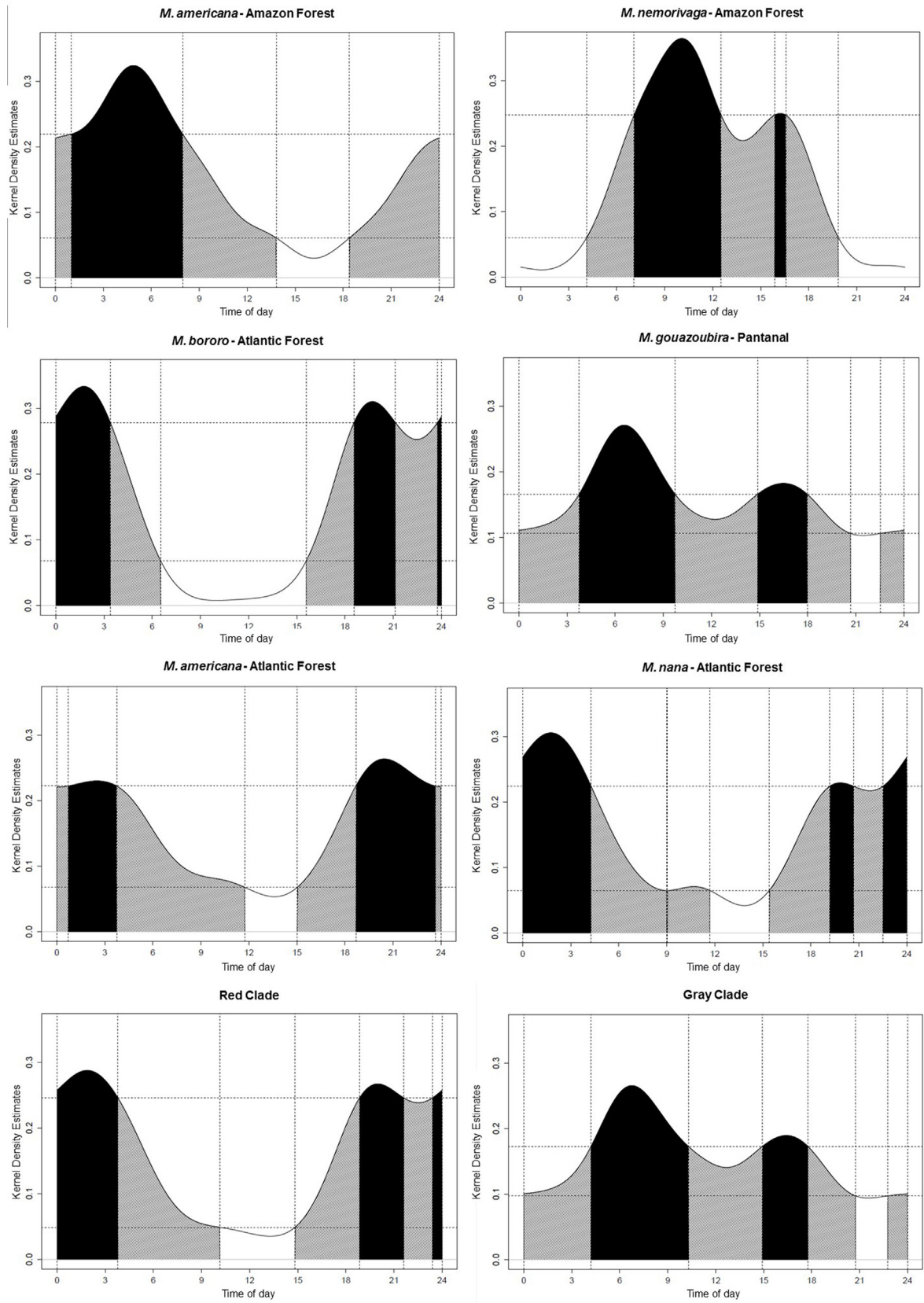


Fig. 3. Circadian rhythm kernel circular analysis for Brazilian *Mazama* and its phylogenetic clades. In grey and black the 0.95 and 0.5 isopleth, respectively.

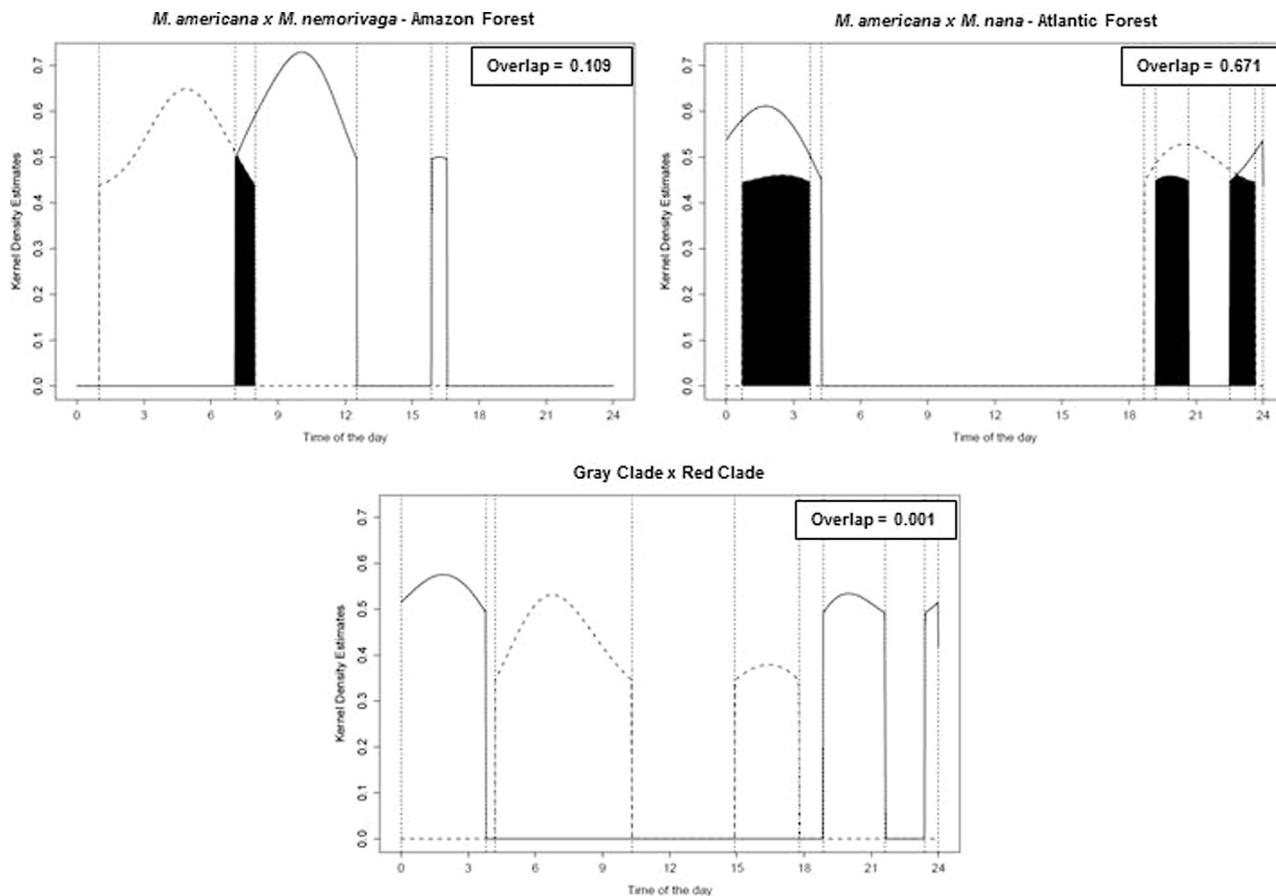


Fig. 4. Activity overlap between the sympatric species and the two phylogenetic clades. In black the species or clade overlap at the 0.5 isopleth activity range. Solid and dotted lines differentiate each species circadian rhythm in each comparison.

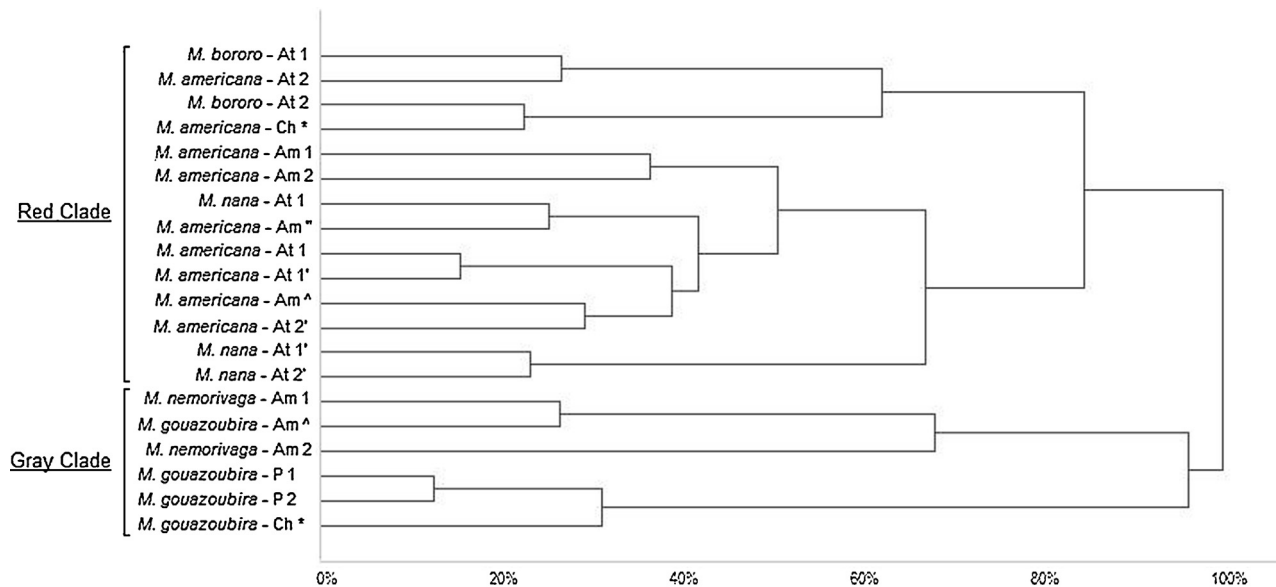


Fig. 5. Cluster Analyses (Complete linkage with Chebyshev distance) performed with the species groups and the percentage of activity in each 2 h class. The numbers 1 and 2 are the group identifications. At = Atlantic Forest, Am = Amazon Forest, P = Pantanal, Ch = Chiquitano Forest. (*) Rivero et al. (2005); (") Gómez et al., 2005; (ˆ) Tobler et al. (2009); (ˆ) Di-Bitetti et al. (2008).

Discussion

Analysis of our results showed that the species of the *Mazama* complex studied have contrasting activity patterns, such that some

species are much more diurnal than others. Even though they inhabit different environments, from the Amazon and Atlantic forested areas to the open lands of the Pantanal, the influence of the habitats only has a marginal effect on the variance in activ-

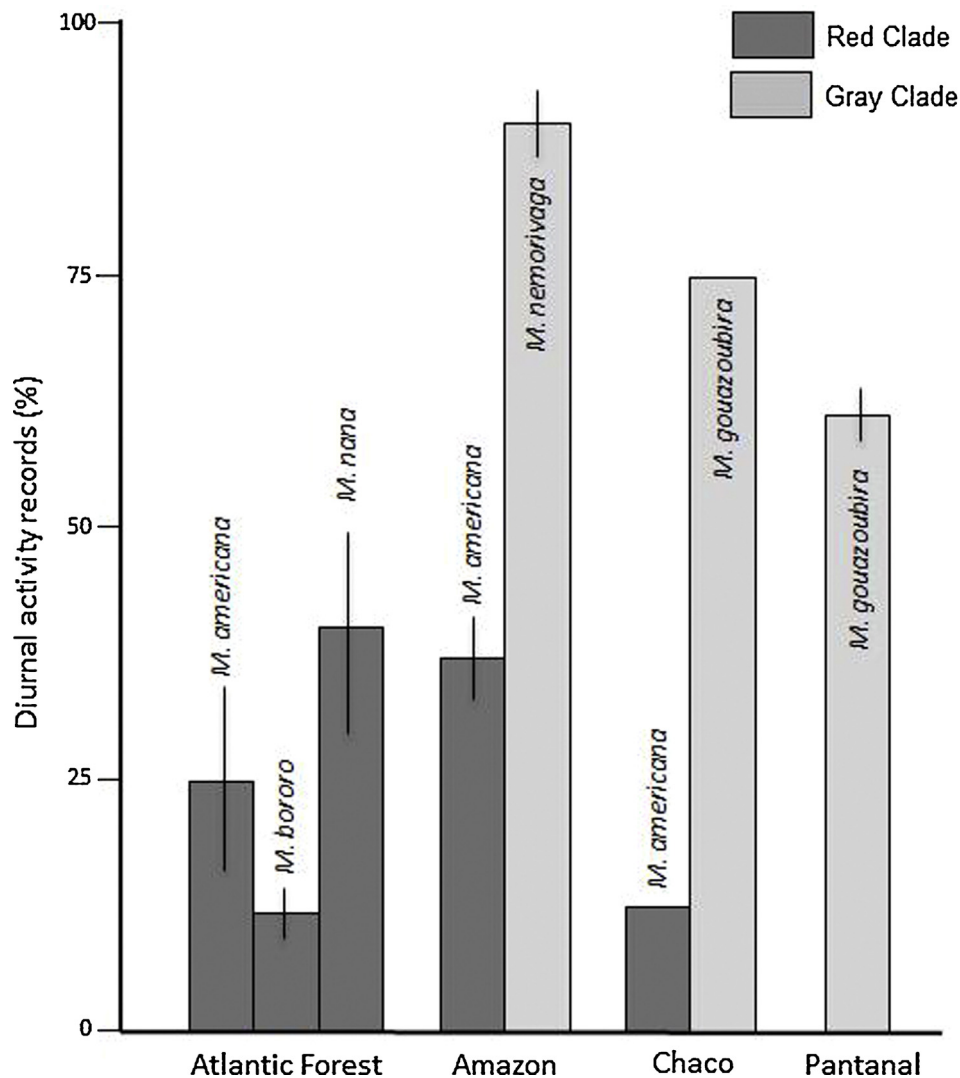


Fig. 6. Percentage of diurnal records for the five *Mazama* species in four habitats. Bars depict standard errors. Dark grey represents the red clade species and light grey represents the grey clade species.

Table 2

Linear Mixed Model results with Diurnal (proportion of diurnal camera shots, including daylight and dawn) transformed with the logit link function as the dependent variable and Clade (red and grey) and Habitat (Amazon Forest, Chaco, Atlantic Forest and Pantanal) as independent factors. Interaction between Clade and Habitat was not significant. Parameter estimates are from the reference category (shown in brackets).

| Effects | df | F | P |
|-----------|---------|--------|-------|
| Intercept | 1, 7.45 | 0.009 | 0.926 |
| Clade | 1, 7.74 | 32.019 | 0.001 |
| Habitat | 3, 7.54 | 3.677 | 0.066 |

| Parameter | Estimate | SE | t | P |
|----------------------------|----------|-------|-------|-------|
| Clade Red (Grey) | -3.140 | 0.555 | 5.659 | 0.001 |
| Amazon (Pantanal) | 2.168 | 0.785 | 2.760 | 0.028 |
| Chaco (Pantanal) | 0.686 | 0.868 | 0.791 | 0.453 |
| Atlantic Forest (Pantanal) | 1.706 | 0.906 | 1.883 | 0.101 |

ity patterns; clade assignment and species appeared as the main predictors of activity rhythms.

Both our own field data and those from other studies were consistent in showing these differences between clades. Species belonging to the red clade showed more nocturnal activity than those of the gray clade in the areas where we conducted fieldwork. Nocturnal activity for species of the red clade was also recorded in the Chiquitano Forest in Bolivia (Rivero et al., 2005), the Amazon Forest in Peru (Tobler et al., 2009), in north Bolivia (Gómez et al.,

2005) and the Atlantic Forest (Di-Bitetti et al., 2008). This last study reported some daylight activity for *M. nana*. The grey clade species showed diurnal activity in both the Amazon Forest and the Pantanal, as also reported for the Chiquitano Forest (Rivero et al., 2005), the Amazon Forest in Peru (Tobler et al., 2009) and the secondary forest in Tucuman, Argentina (Black-Décima, 2000).

Late-morning centred activity was observed for *M. nemorivaga*, in contrast with *M. gouazoubira*, which was more active in the early morning and late afternoon. This difference could be explained

Table 3
Linear Mixed Model results with Diurnal (proportion of diurnal camera shots, including daylight and dawn) transformed with the logit link function as the dependent variable and Species and Habitat as independent factors. Parameter estimates are from the reference category (shown in brackets).

| Effects | df | F | P |
|-----------|---------|--------|-------|
| Intercept | 1, 3.56 | 4.911 | 0.099 |
| Species | 4, 3.54 | 13.880 | 0.018 |
| Habitats | 3, 3.95 | 5.369 | 0.070 |

| Parameter | Estimate | SE | t | P |
|--|----------|-------|-------|-------|
| <i>M. americana</i> (<i>M. nemorivaga</i>) | −2.715 | 0.614 | 4.425 | 0.021 |
| <i>M. bororo</i> (<i>M. nemorivaga</i>) | −3.990 | 0.887 | 4.499 | 0.019 |
| <i>M. gouazoubira</i> (<i>M. nemorivaga</i>) | 0.695 | 0.712 | 0.977 | 0.386 |
| <i>M. nana</i> (<i>M. nemorivaga</i>) | −2.533 | 0.822 | 3.083 | 0.047 |
| Amazon (Pantanal) | 2.486 | 0.712 | 3.492 | 0.027 |
| Chaco (Pantanal) | 0.821 | 0.712 | 1.154 | 0.315 |
| Atlantic Forest (Pantanal) | 2.191 | 0.833 | 2.628 | 0.062 |

by the very high exposure to solar radiation during the middle of the day that *M. gouazoubira* experiences in the warm open lands of the Pantanal (daily temperature varies up to 18 °C), while for *M. nemorivaga*, the dense Amazon forest likely acts as a buffer narrowing the daily thermal range that is up to 13 °C. The high overlap (0.671) between *M. americana* and *M. nana* in their activity peaks suggests that another niche axis (e.g. diet, fine-scale habitat use), instead of the time axis, allows them to coexist, as indicated by Vogliotti (unpublished results). The opposite situation was observed between *M. americana* and *M. nemorivaga* in the Amazon Forest, where little overlap occurred (0.109). In the absence of any hypotheses concerning possible niche segregation on the basis of space or diet, these differences in sympatry also indicate a predominant role of phylogenetic effects on circadian rhythms.

Cluster and Mixed Model analyses support the stronger effect of phylogeny over habitats. The habitats did not match the cluster indicating that their effect was not as strong as that of clades. The occurrence of branches for sites within a species in different groups in the cluster analyses indicates some intraspecific variation in the circadian rhythm, for *M. americana* for example, that does not discard a possible habitat effect.

Mazama species constitute a polyphyletic group that comprises separate phylogenetic lineages that experienced a process of evolutionary convergence when adapting to similar forested habitats in the neotropics (Duarte et al., 2008). The convergence process affected species morphology, with a small body size and minimal sexual dimorphism corresponding to behavioural adaptations that include solitary social behaviour, exclusive use of territories and a little polygynous mating system. Morphology both in the Cervidae and in African ungulates is clearly related to the environment where they live, such that small size and minimal dimorphism and behaviours that include solitary life, territories and low polygyny are common adaptations to forest habitats (Jarman, 1974; Geist, 1998; Pérez-Barbería et al., 2002).

If selection pressure in neotropical forests has acted on morphological and behavioural features of Cervidae species belonging to different lineages, this raises the question of why this convergent process appears not to have affected the activity rhythms: why have activity rhythms not converged into an optimal pattern in all the species adapting to the same ecosystems? There may be several possible explanations.

One of the reasons may be that both lineages evolved in different environmental conditions favouring divergence in activity rhythms over the last 2.5 million years after they crossed the Panama isthmus, even though they currently mostly occur in forested habitats. In general, South America has experienced pulses of colder-arid and warmer-moistened conditions during the last 150,000 years, and both forests and open lands have always occurred in large areas in the subcontinent (Haffer, 1969; De Vivo and Carmignotto, 2004).

For instance, open areas seem to have shaped the morphology and behaviour of genera like *Odocoileus*, *Ozotoceros* and *Blastocerus*. However, *Mazama* species do not match this adaptation features to open areas, but even so, we may speculate that adaptation to different forest types or habitats within the forests might be responsible for observed clade differences in activity patterns within the genera.

Another possible explanation is that for any group of species using the same habitat, there is a selective force to split the temporal niche, for example to reduce competition (Hardin, 1960). In the case of small, forest-dwelling herbivores, the competition for food is probably very low (e.g. roe deer in European forests: Andersen et al., 1998). Brouck deer might experience some competition for fruit, but it is unlikely that circadian segregation would reduce it. Alternatively, temporal segregation may be favoured as an antipredatory strategy, since in closed habitats, solitude, inconspicuous morphology and small body size could contribute to reducing the risk of predation (Nowak, 1999). However, refuting this explanation, we found no temporal segregation when two or more species from the same clade (e.g. *M. americana* and *M. nana*) occur in the same habitat, only when species from different clades do.

Finally, phylogenetic inertia and constraints, along with some benefit from temporal segregation, may prevent the effect of potential selective forces for an environment-specific activity rhythm, thus maintaining clade-specific patterns in any habitats. Our results appear more compatible with this explanation and it could be stated that this is a case of phylogenetic signal or phylogenetic niche conservatism (Wiens, 2004). The definitions of these concepts have been discussed by Losos (2008).

It is generally acknowledged that some taxa are mainly diurnal and others are nocturnal. In placental mammals, for example, some orders are predominantly diurnal, nocturnal or present both activity patterns (Nowak, 1999). Phylogenetic imprint can be a strong constraint for variation in activity patterns, as has been shown for rodents (Roll et al., 2006). Circadian rhythms in *Mazama* clades also seem to be a case of a phylogenetic constraint on behaviour. This poses another question as to why the evolutionary history of both clades favoured different circadian rhythms. In rodents, it seems that clades adapted to colder regions evolved more diurnal patterns (Roll et al., 2006). Although *Mazama* species may have adapted to very similar habitats, the ancestral lineages to which they belong may have evolved under different conditions. Species from the grey clade share ancestors with the genera *Hippocamelus*, *Blastocerus*, *Ozotoceros*, which are mainly diurnal (González et al., 2010; Piovezan et al., 2010; Vila et al., 2010), while species from the red clade share ancestors with the white-tailed-deer (*Odocoileus virginianus*), which is an extremely adaptable species and has a flexible circadian rhythm with morning and/or crepuscular and/or evening

activity (Gallina et al., 2010). All these ideas suggest a hypothesis, deserving of further research, for a greater tendency towards diurnal activity in the ancestors of the grey clade that may have influenced the patterns observed for *M. gouazoubira* and *M. nemorivaga*.

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