



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

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