

Temporal partitioning facilitates the coexistence of carnivore mammals in a large but isolated Atlantic Forest remnant

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Abstract

Temporal partitioning is an important mechanism for carnivore mammals that live in sympatry in current forest remnants. We evaluated whether temporal partitioning would facilitate coexistence among carnivores in a tropical forest and its adjacent human-related area, as well as if there is a possible correlation between the activity patterns of these carnivores and their potential prey. We used camera traps and circular statistics to explore the degree of temporal overlap between dominant and subordinate predators, as well as between predators and their potential preys. Pumas (*Puma concolor*) were less active when jaguars (*Panthera onca*) were more active. Overall, ocelots (*Leopardus pardalis*) and crab-eating foxes (*Cerdocyon thous*) presented either a strong or a weak temporal partitioning with jaguars and pumas, respectively, but apparently spatial or dietary segregation might facilitate more their coexistence with these large predators. Tayras (*Eira barbara*) and coatis (*Nasua nasua*) were diurnal and, therefore, did not overlap temporally with nocturnal carnivores, except pumas. In the human-related area, ocelots were mostly nocturnal and pumas diurnal, probably due to the temporal activity of their related preys. Our findings suggest that temporal partitioning may allow coexistence between our studied predators in one of the largest Atlantic Forest remnant in Brazil, but preys have an important role, shifting the activity pattern of their predators according to the studied area.

INTRODUCTION

The coexistence between species with similar ecological niches is allowed by the partitioning of the niche requirements between the species involved, being the spatial, dietary, and temporal dimensions the most common mechanisms of segregation (Schoener 1974). Temporal partitioning is more common among predators, since their prey shows peaks of activity, unlike herbivores, where plants and its parts can be found at any time (Schoener 1974). Temporal partitioning is especially important for large carnivore mammals, as they have large body-mass and, therefore, larger home ranges (Lindstedt et al. 1986), which do not allow for spatial partitioning in the current scenario of tropical forest depletion worldwide (Keenan et al. 2015). In this scenario, dietary partitioning is also unlikely, since smaller remnants support fewer species (Pardini et al. 2005; Cáceres et al. 2014) that could be a potential prey for medium- to large-sized carnivores. Therefore, temporal partitioning might be an important strategy for the coexistence between large carnivores in the current forest remnants.

The lack of an efficient niche partitioning between carnivores can lead to an Intraguild Predation (IGP) or Interspecific Killing (IK; Polis et al. 1989). IGP occurs when the dominant predator kills and eats the subordinate predator that uses similar resources, thus reducing competition, whereas IK occurs when the dominant predator kills the subordinate predator without any immediate energy gain to the dominant predator (Polis et al. 1989). The species with the highest body-mass is the dominant predator on the IGP/IK relationships and the smaller (and subordinate) predators are directly affected, a phenomenon that can directly influence the community structures (Polis et al. 1989) and may even result in local species extinction.

To avoid competition, subordinate predators can change their temporal activity, diet, and habitat use according to the specific conditions of each location at each time. This is possible because the niche of the subordinate predator is generally broader than the niche of the dominant predator, which is embedded into the niche of former species (Polis et al. 1989). However, few cases of complete inversion in the activity pattern were reported among mammals, perhaps because of the phylogenetic constrain of species, as observed in rodents by Roll *et al.* (2006). Usually, changes in the temporal activity or its limitation that acts as a response to the predation risks, thus reducing forage and energy gain by the subordinate competitor (Kronfeld-Schor and Dayan 2003).

The Atlantic Forest is an excellent biome for studying temporal partitioning between predators. It was greatly reduced and fragmented in the last decades, with few remaining areas of continuous native forest, and is currently composed primarily by fragments with less than 50 ha (Ribeiro et al. 2009). Among other smaller predators, there are two species of large predators that inhabit the Atlantic Forest: the jaguar (*Panthera onca*) and the puma (*Puma concolor*). Jaguars lost most of its historical distribution (Tôrres et al. 2008), but they are still present in some large Atlantic Forest remnants, while pumas have a broader current distribution in the biome (Beisiegel et al. 2012).

Most studies with these two large felids found great similarities between their activity patterns, as in Argentina (Di Bitetti *et al.* 2010), Belize (Harmsen *et al.* 2009; Harmsen *et al.* 2011), Brazil (Gómez *et al.* 2005; Foster *et al.* 2013), Mexico (Núñez *et al.* 2002), and Venezuela (Scognamillo *et al.* 2003). Conversely, there were no significant differences between their activity patterns in some cases (Romero-Muñoz *et al.* 2010; Blake *et al.* 2012). Usually, the temporal partitioning between jaguars and pumas was either associated with species avoidance (Romero-Muñoz *et al.* 2010) or activity synchronization with their main prey (Blake *et al.* 2012).

The temporal activity pattern of jaguars and pumas can also be influenced by the environment characteristics. Paviolo *et al.* (2009) found the higher nocturnal activity of pumas in areas where hunt pressure was higher in comparison with more protected areas, which might be a strategy to avoid conflict with humans, as also observed with other predators (Schuette et al. 2013; Massara et al. 2018). The temporal activity of predators may also be influenced by the temporal activity of their preys. The relationship between the temporal activity of predators and their prey might be linked either to the predation risk of the prey, or an alignment of the predator temporal activity to the activity peaks of their prey, which is related to coevolution strategies (Kronfeld-Schor and Dayan 2003). The synchronization with the temporal activity of preys is advantageous for predators since they can optimize its energy use foraging in a day period when their preys are more active.

There are several studies of temporal partitioning between other terrestrial carnivore mammals in the Neotropics with varied results (Di Bitetti et al. 2009; Massara et al. 2016; Ramírez-Mejía and Sánchez 2016), especially on ocelots (*Leopardus pardalis*) and other smaller felids (Lucherini et al. 2009; Blake et al 2012; Massara et al. 2018; Santos et al. 2019). The temporal activity pattern of these smaller carnivores depended mainly on their habitat characteristics (i.e., prey availability and human disturbance level) and the presence of potential competitors.

We aimed to evaluate whether the coexistence of terrestrial mammal carnivores may be facilitated by temporal partitioning in an isolated Atlantic Forest remnant. We expected jaguars, the largest predator, to influence the activity patterns of all other predators, which may temporally segregate with jaguars to avoid IGP or IK. We also expected the same strategy for all the remaining predator relationships, where dominant predators may influence the temporal activity of the subordinate predators. Since some predators are naturally diurnal, we expected them to segregate temporally with nocturnal predators. We also expected nocturnal predators to be mostly or exclusively nocturnal in human-related locations, as a more nocturnal activity reduces the chances of encounters with humans that are usually more active during the daylight. Lastly, because differences in the temporal activity patterns are not necessarily relate with competition strategies to avoid dominant predators, we also evaluated whether the temporal activity of predators could be a strategy to maximize their chances to find potential preys, as observed by several studies with neotropical

felids (Harmsen *et al.* 2011; Foster *et al.* 2013; Nagy-Reiset *et al.* 2019).

MATERIALS AND METHODS

Study site — The study was conducted in two adjacent areas with distinct protection categories (Figure 1). The Rio Doce State Park (RD) is an IUCN protected area category II (National Park) and the largest remnant of Atlantic Forest of State of Minas Gerais, southeastern Brazil, with ca. 36,000 ha of stational semi-deciduous forest (SOS Mata Atlântica 2019). The RD has a large lacustrine system composed of 42 natural lakes and it is limited in the eastern part by the Rio Doce river. In 2010 the RD importance was internationally recognized when it became a Ramsar site by UNESCO's Convention on Wetlands. Despite being one of the largest remnants of Atlantic Forest, RD is isolated from other forest remnants and is surrounded by several types of human-related habitats, especially a mosaic formed by eucalyptus plantations, but also native forest fragments.

The second study area (EP) is a private property of ca. 23,000 ha composed mainly by eucalyptus plantations, but also by fragments of Atlantic Forest and natural lakes. This area is an IUCN protected area category VI (Protected area with sustainable use of natural resources) and during the evaluation time, eucalyptus management and logging were regularly done. Hunting is prohibited either in RD or in EP, but fishing is allowed in EP lakes, where fishermen and illegal hunters are common. The EP area is located at the southern border of the RD buffer zone, and it is commonly frequented by mammals. The region has a tropical climate and during this study had an annual precipitation of 1,035 mm and the average temperature was 25°C (INMET 2019).

Data collection — Sample period was from April 2014 to January 2015, where camera traps (Bushnell®) were deployed on man-made trails and game trail in RD and EP, totalizing 30 camera sites (15 on each area). A minimum distance between camera sites was 1km to minimize a lack of independence between sampling sites. Camera traps were deployed 30cm above ground level, allowing the detection of medium- to large-sized mammals, and operated 24-h.

Activity patterns analysis — We defined an activity sample as all photographs of the same species detected at a camera site within an 1-h period, thus minimizing the nonindependence of consecutive photographs. The hour of each activity sample recorded by the camera traps was transformed into a solar time based on sunrise and sunset times of our study area. This is important to accurately define the activity pattern of the species and also to allow comparisons with other studies (Foster *et al.* 2013). Sunrise and sunset times were obtained from the software Moonrise v.3.5 (Romero-Muños *et al.* 2010; Foster *et al.* 2013), and we used the following formula described by Woolf (1968) for solar conversion:

$$LCT = t_s - \frac{EOT}{60} + LC + D$$

Where LCT is the standard clock time, t_s the solar time, EOT the equation of time, LC the longitudinal correction, and D the daylight saving time (see Woolf (1968) for further details).

Then, we used the Rao's spacing test (Rao 1976) to verify whether the species activity pattern was uniformly distributed (i.e., cathemeral) or associated with a specific time period (i.e., diurnal, nocturnal or crepuscular). We categorized the activity pattern of each species into diurnal (>60% of records between 1h after the sunrise and 1h before the sunset), nocturnal (>60% of records between 1h after the sunset and 1h before the sunrise), crepuscular (>50% of records occurring 1h before and after sunrise and sunset) and cathemeral (peaks of activity through the diurnal and nocturnal period). To compare the 24-h cycles of each species between RD and EP we used the Mardia-Watson-Wheeler test (W). When the W test revealed no significant differences ($P > 0.05$) in the 24-h cycles of a given species between the studied areas, we combined species data from both areas for the subsequent analyses. The analyses were performed using the package "circular" v.0.4-93 (Lund and Agostinelli 2017) in R Software v.3.6.3 (R Development Core Team 2019).

Activity overlap analysis — To evaluate the temporal activity overlap between predators, as well as between predators and their potential prey, we calculated the coefficient of overlap (Δ ; Ridout and Linkie 2009) that varies from 0 (no overlap) to 1 (complete overlap). We used the Δ_1 estimator when the number of independent records of at least one species in the pairwise comparisons was <75 photographs. Otherwise, we used the Δ_4 estimator. We calculated the 95% confidence intervals for $\hat{\Delta}$ from 10,000 bootstrap samples (Ridout and Linkie, 2009). To complement the coefficient of overlap, we compared the 24-h cycles between species using the W test. To calculate the coefficient of overlap and the W test statistics we used the package “overlap” v.0.3.2 (Linkie and Ridout 2011) and the package “circular” respectively, both available in the R Software.

Potential preys were based on studies of feeding habits for each predator species (Appendix 1). We considered as potential preys only those preys found at least once in any study. Rarely, some prey species that are much larger than the predator were described as a diet item, but as it was related to a scavenging behavior, we did not consider it directly as a potential prey. We did not find in any study that the giant-armadillo (*Prionomys maximus*) could be a prey item for jaguars, but because we believe that this predator can prey upon it, we included the giant-armadillo as potential prey for jaguars.

We used the study of Oliveira and Pereira (2014) to either verify the relationships of dominance and subordination among predators or the possibilities of IGP/IK among them. The analysis of temporal activity overlap was performed only if either IGP or IK was noticed between the given predators in this study. Also, according to this study, jaguars are the top predators with no natural predators. The puma has the jaguar as a potential predator, and ocelots have jaguars and pumas as potential predators. These three felids are potential predators for crab-eating foxes, tayras, and coatis, and there were no records of IGP or IK between these latter species.

RESULTS

A total of 1796 photographs were recorded (1004 in RD, 792 in EP), with a sampling effort of 3710 camera traps day (Table 1). Records of *Mazama americana* (red brocket) and *M. gouazoubira* (gray brocket) were combined due to difficulties in differentiate both species using our photograph registers. Six out of the 16 species analyzed showed a significantly difference in the temporal activity pattern between both areas (Appendix 2). Even though ocelots and South American tapirs (*Tapirus terrestris*) were mainly nocturnal, they presented more diurnal records in RD (Table 1). Pumas and deers were nocturnal in RD, but cathemeral in EP (Table 1). Tapetis (*Sylvilagus brasiliensis*) and collared peccaries (*Pecari tajacu*) could not be classified according to activity pattern categorizations. Tapetis were nocturnal in EP, but in RD presented also crepuscular activities (Table 1). Peccaries were diurnal in RD, but in EP presented also nocturnal and crepuscular activities (Table 1).

The 24-h cycles for ten species were not significantly different between RD and EP and, therefore, records from both areas for these species were combined. For predators, jaguars and crab-eating-foxes were nocturnal, whereas tayras and coatis were diurnal (Table 1). For the potential preys, big-eared opossums (*Didelphis aurita*), nine-banded armadillos (*Dasypus novemcinctus*), lowland pacas (*Agouti paca*), lesser anteaters (*Tamandua tetradactyla*), and giant armadillos were nocturnal (Table 1). The Azara’s agouti (*Dasyprocta azarae*) was the only diurnal species (Table 1).

Although we found an overlap between the temporal activity of predators, the W test revealed dissimilarities (Figure 2) in the following pairwise comparisons: jaguars and pumas in EP, with less overlap during the daylight as jaguars were nocturnal and pumas cathemeral; jaguars with tayras and coatis in both areas, where the latter subordinate species were diurnal with low overlap with jaguars; pumas with ocelots and crab-eating-foxes in EP, where pumas used more of the daylight than the latter species; pumas and tayras in both areas, especially during the crepuscular hours, where tayras had a higher activity; pumas and coatis in RD, with little overlap during the daylight; and ocelots with tayras and coatis in both areas, with low overlap during the daylight. The W test revealed no significant differences between the temporal activity of predators in the following pairwise comparisons: jaguars and ocelots in both areas; jaguars and crab-eating-

foxes in both areas; jaguars and pumas in RD; pumas and ocelots in both areas; pumas and crab-eating-foxes in RD; pumas and coatis in EP; and ocelots with crab-eating-foxes in both areas.

The overlap between the temporal activity of predators and their potential preys was diverse, and the W test revealed no significant dissimilarities (Figure 3) in the following pairwise comparisons: jaguars in both areas with opossums, anteaters, giant armadillos, nine-banded armadillos, tapirs, and pacas; jaguars with tapetis in EP and with deers in RD; pumas with peccaries in EP and with pacas in RD; pumas with deers in both areas; ocelots with anteaters and pacas in both areas; ocelots with opossums and nine-banded armadillos in EP; and crab-eating-foxes with tapetis in EP. Conversely, the W test revealed significant dissimilarities (Appendix 3) in the following pairwise comparisons: jaguars with agoutis and peccaries in both areas; jaguars with tapetis in RD and with deers in EP; pumas in both areas with opossums, anteaters, nine-banded armadillos, tapetis, and agoutis; pumas with peccaries in RD and with pacas in EP; ocelots in both areas with tapetis and agoutis; ocelots in RD with opossums and nine-banded armadillos; crab-eating-foxes in both areas with opossums and agoutis; and crab-eating-foxes with tapetis in RD. Tayras and coatis are not known to prey upon medium- to large-sized mammals.

DISCUSSION

Although we found a high activity overlap between jaguars and pumas, such as other studies (Scognamillo *et al.* 2003; Harmsen *et al.* 2009; Harmsen *et al.* 2011; Foster *et al.* 2013), their activity pattern was significantly dissimilar. Corroborating the findings of Hernández-SaintMartín *et al.* (2013), we also observed a negative correlation between the peak of activity of jaguars and the peak of activity of pumas. Pumas used much more of the daylight compared to jaguars, especially in EP. This can be characterized as a time partitioning between these predators, where pumas might be negatively influenced by having smaller body sizes (Iriarte *et al.* 1990). Therefore, as pumas are subordinate to jaguars, they tend to avoid the peak of the activity of jaguars to reduce the probabilities of IGP and IK.

However, different temporal activity patterns, such as the case of jaguars and pumas, may allow each predator to make use of different preys more efficiently and thus, facilitate coexistence between competing species. Although we did not sample important prey species for jaguars, such as capybaras and caimans, this predator overlapped temporally with eight prey species in our studied area. Contrary, pumas are temporally overlapped with pacas in RD, with peccaries in EP, and in both areas with deers. The temporal overlap between the puma activity and the deer activity is not a surprise as deers are commonly found in puma's diet (Scognamillo *et al.* 2003; Novack *et al.* 2005; Moreno *et al.* 2006), and the shift in the activity pattern found for pumas (i.e., nocturnal in RD, but cathemeral in EP) might be related to the deer activity patterns. Red brocket deers prefer forested areas (i.e., RD) and are nocturnal, whereas gray brocket deers are more generalist and diurnal (Ferregueti *et al.* 2015). Therefore, it is possible that pumas increase the likelihood of preying on red brockets in RD by using more of the nighttime and gray brockets in EP by using more of the daytime. This shift in the activity pattern found for pumas reinforce the high plasticity of the species to adapt to different environmental conditions (De Angelo *et al.* 2011; Moss *et al.* 2016).

Ocelots with jaguars showed a high and significant temporal overlap in all areas and in RD with pumas, suggesting that coexistence might be facilitated by differences in other niche dimensions (Davies *et al.* 2010) or even facilitated by the low density of jaguars in our study area (Viana 2006), which might result in few encounters with this species (Davies *et al.* 2010). Also, ocelots prey mainly on rodents (Meza *et al.* 2002; Moreno *et al.* 2006; Booth-Binczik *et al.* 2014) but can prey on primates (Bianchi and Mendes 2007; Abreu *et al.* 2008; Bianchi *et al.* 2010). Importantly, smaller preys are selected by ocelots when in sympatry with jaguars (Moreno *et al.* 2006). Therefore, ocelots are probably limited to smaller preys in our studied areas, which may reduce competition with the larger felids in this potentially competitive scenario, where ocelots are clearly a victim of IGP and IK due to its smaller body mass (Oliveira and Pereira 2014).

Crab-eating-foxes with jaguars, pumas, and ocelots showed a significant temporal activity overlap, but the species prefers areas with intermediate forest cover and broader trails (Goulart *et al.* 2009), which are characteristics found in EP. The crab-eating-fox activity pattern was dissimilar from pumas in EP, which

combined to the low density of jaguars, may result in low risks of IGP and IK. Also, the great body mass differences with jaguars and pumas and the low density of jaguars may result in low risks of IGP and IK. Similarly, the small body mass difference between crab-eating-foxes and ocelots may reduce IGP and IK risks. Therefore, because the IGP and IK risk for the crab-eating-fox are unlikely, the species may benefit greatly for hunting preys (i.e., tapetis) in EP.

As expected, tayras showed a diurnal activity pattern and, therefore, no significant overlap was found with the temporal activity pattern of jaguars, pumas, and ocelots. Although mustelids have one of the highest competitive pressure among the American carnivore families, tayras are omnivorous and can use arboreal strata and aquatic environment, which may facilitate the coexistence with dominant predators (Hunter and Caro 2008).

Coatis with pumas in EP showed a significant temporal activity overlap, but as coatis are mainly diurnal, have an omnivorous feeding habits, and frequently uses the arboreal strata, it present low risks of IGP and IK by pumas. This is somehow expected, given the lowest competition pressure among the American carnivores of the Procyonidae family, possibly due to their ability to change the spatial and temporal use of resources (Hunter and Caro 2008).

Contrary to our initial hypothesis, most predators did not show less diurnal activity where human activity was higher (i.e., EP). Jaguars and coatis showed similar temporal activity in RD and EP. The few records of crab-eating-foxes and tayras did not allow us this comparison, but crab-eating-foxes only occasionally use RD. Only ocelots were more nocturnal in EP, but this might be a response to the tapetis activity pattern, an important and apparently abundant prey that also was more nocturnal in EP. Of course, this higher nocturnal activity of ocelots in EP also might result in fewer encounters with both pumas and humans, which was suggested to be a mechanism (or strategy) adopted by ocelots to allow its coexistence with pumas and humans in Atlantic Forest remnants (Massara et al., 2018). Surprisingly, pumas were more diurnal where the human activity is higher (i.e., EP), contradicting other studies (Paviolo et al. 2009; Carter et al. 2012; Schuette et al. 2013). We have two hypotheses to explain this result. Firstly, both study areas are so isolated and saturated with predators that competition is high and the benefits of hunting during the daytime outweigh the risks of encountering humans. Secondly, human activities in EP may not be as intense as we expected and because the eucalyptus management is limited mainly to smaller areas at each given time thus, leaving the rest of the area untouched, the encounters with humans are unlikely.

We observed that temporal partitioning contributes to the coexistence among predators in our studied areas. Pumas avoided conflicts with jaguars by using more the daytime, which increased also the likelihood of encountering diurnal preys, especially in EP. Ocelots avoided conflicts with pumas in EP by being more nocturnal, but the coexistence in RD with jaguars must be facilitated by the different use of preys. Tayras and coatis were diurnal, which might result in a low probability of agonistic encounters with nocturnal felids, besides the different niches among them. The temporal partitioning seemed unimportant only for crab-eating-foxes, but they probably coexist with felids by using the habitat and preys differently. In other words, our findings suggest that temporal partitioning contributed to the coexistence of predators by shifting the temporal activity pattern of the subordinate predator to hours that the dominant predator is less active, thus reducing the chances of direct conflicts. The shift in the activity pattern by the subordinate predator may also contribute to reducing competition by increasing its chances of encountering different preys.

However, in some cases the temporal partitioning did not occur or it was very subtle, since it depends on some other factors (or variables), such as the density of the dominant predators (Durant 1998; Davies et al. 2010), the other niche dimensions (e.g., diet) (Davies et al. 2010), the prey availability (Carrillo et al. 2009), and the human activities (Paviolo et al. 2009; Carter et al. 2012; Schuette et al. 2013), which needs to be investigated by further studies. We suggest that future studies use a combination of the spatial (e.g., telemetry data), temporal and trophic (e.g., diet data) dimensions of the niche to evaluate the drivers that may facilitate species coexistence in the Atlantic Forest fragments. Also, it is reasonable to expect that species will respond differently to human activities and matrix type and thus, these studies should also consider natural patches in different disturbance scenarios, which may also favor (or not) species dispersal. These studies are even

more urgent for those more specialist species, such as jaguars, which are more susceptible to extinction in the current scenario of the Atlantic Forest.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHORS CONTRIBUTIONS

RH and FR conceived the ideas and designed methodology; RH executed the experiment and analyzed the data; RM assisted with the data analysis; RH led the manuscript writing; FR and RM assisted with the manuscript writing.

DATA ACCESSIBILITY STATEMENT

- *Species occurrence with time and location of the records: Dryad doi: 10.5061/dryad.r4xgxd28m

* Dataset is private for peer review, but available for reviewers at the following URL: <https://datadryad.org/stash/share/DQ5oWileQw9MfkKcyceivssR7pn0Mmufdd7kJ-7IOPg>

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FIGURE LEGENDS

Figure 1. Camera trap locations used for sampling medium- to large-sized terrestrial mammals from April 2014 to January 2015 in Rio Doce State Park (RD) and its adjacent areas of eucalyptus plantations, southeastern Brazil.

Figure 2. Coefficients of overlap (Δ) between the temporal activity of medium- to large-sized terrestrial carnivore mammals sampled in Rio Doce State Park (RD), in its adjacent areas of eucalyptus plantations (EP), and in both areas combined if no area is specified. The lines inside the charts are the temporal activity of each predator, where the continuous line (—) is representing the dominant predator, and the dotted line (...) the subordinate predator. Overlap between activity periods is represented by the shaded area. The x-axis represents the time of the day in 24h format. The y-axis range is the activity's density of the species. “W” is the statistics for the Mardia-Watson-Wheeler test between the pairwise comparisons.

Figure 3. Coefficients of overlap (Δ) between the temporal activity of medium- to large-sized terrestrial carnivore mammals and their prey sampled in Rio Doce State Park (RD), in its adjacent areas of eucalyptus plantations (EP), and in both areas combined if no area is specified. The lines inside the charts are the temporal activity of each species, where the continuous line (—) is representing the predator, and the dotted line (...) the prey. Overlap between activity periods is represented by the shaded area. The x-axis represents the time of the day in 24h format. The y-axis range is the activity's density of the species. “W” is the statistics for the Mardia-Watson-Wheeler test and it is presented only between the pairwise comparisons where none dissimilarities were found.

TABLES

Table 1. Activity patterns of medium- to large-sized terrestrial mammals sampled in Rio Doce State Park (RD) and its adjacent areas of eucalyptus plantations (EP) from April 2014 to January 2015. “D%”, “N%”,

and “C%” are percentage of diurnal, nocturnal and crepuscular records, respectively. “H” is the activity pattern of the species (“c” for cathemeral, “d” for diurnal, “n” for nocturnal, and “s” for special cases where we could not classify the activity pattern according to our categorization approach). “U” is the Rao’s spacing test statistics value.

Species	Site	<i>n</i>	D (%)	N (%)	C (%)	H	<i>U</i>	<i>P</i>
<i>Panthera onca</i>	RD+EP	27	4 (15)	20 (74)	3 (11)	n	160.28	<0.05
<i>Puma concolor</i>	RD	92	12 (13)	57 (62)	23 (25)	n	240.07	<0.001
<i>Puma concolor</i>	EP	21	8 (38)	8 (38)	5 (24)	c	154.88	>0.05
<i>Leopardus pardalis</i>	RD	139	22 (16)	93 (67)	24 (17)	n	172.28	<0.001
<i>Leopardus pardalis</i>	EP	63	3 (5)	54 (86)	6 (10)	n	174.98	<0.001
<i>Cerdocyon thous</i>	RD+EP	30	2 (7)	23 (77)	5 (17)	n	184.57	<0.001
<i>Eira barbara</i>	RD+EP	25	17 (68)	1 (4)	7 (28)	d	166.80	<0.05
<i>Nasua nasua</i>	RD+EP	36	22 (61)	2 (6)	12 (33)	d	157.94	<0.05
<i>Didelphis aurita</i>	RD+EP	87	1 (1)	79 (91)	7 (8)	n	196.17	<0.001
<i>Tamandua tetradactyla</i>	RD+EP	14	1 (7)	11 (79)	2 (14)	n	169.16	<0.05
<i>Priodontes maximus</i>	RD+EP	19	1 (5)	16 (84)	2 (11)	n	218.85	<0.001
<i>Dasybus novemcinctus</i>	RD+EP	158	1 (1)	151 (96)	6 (4)	n	221.82	<0.001
<i>Sylvilagus brasiliensis</i>	RD	124	2 (2)	70 (56)	52 (42)	s	240.07	<0.001
<i>Sylvilagus brasiliensis</i>	EP	49	0	39 (80)	10 (20)	n	229.55	<0.001
<i>Tapirus terrestris</i>	RD	278	32 (12)	176 (63)	70 (25)	n	159.55	<0.001
<i>Tapirus terrestris</i>	EP	336	19 (6)	238 (71)	79 (24)	n	180.38	<0.001
<i>Pecari tajacu</i>	RD	27	19 (70)	5 (19)	3 (11)	d	180.10	<0.01
<i>Pecari tajacu</i>	EP	31	14 (45)	9 (26)	8 (26)	s	182.73	<0.001
<i>Mazama sp.</i>	RD	45	12 (27)	30 (67)	3 (7)	n	156.53	<0.05
<i>Mazama sp.</i>	EP	27	12 (44)	7 (26)	8 (30)	c	131.13	>0.05
<i>Cuniculus paca</i>	RD+EP	20	0	19 (95)	1 (5)	n	215.59	<0.001
<i>Dasyprocta azarae</i>	RD+EP	148	113 (76)	1 (1)	34 (23)	d	193.09	<0.001

APPENDICES

Appendix 1. Prey species found on the diet of jaguars (*Panthera onca*), pumas (*Puma concolor*), ocelots (*Leopardus pardalis*), and crab-eating-foxes (*Cerdocyon thous*) at least once among several studies and considered as potential preys for the analyses of temporal activity overlap between predators and preys sampled in Rio Doce State Park and its adjacent areas of eucalyptus plantations, southeastern Brazil.

Species	<i>P. onca</i>	<i>P. concolor</i>
<i>Didelphis aurita</i>	[1] [5]	[5]
<i>Tamandua tetradactyla</i>	[4] [5]	[5] [7]
<i>Dasybus novemcinctus</i>	[1] [2] [3] [4]	[6] [7] [8]
<i>Sylvilagus brasiliensis</i>	[1] [4]	[3] [5] [9]
<i>Tapirus terrestris</i>	[2] [4]	-
<i>Pecari tajacu</i>	[1] [2] [3] [4]	[3] [5] [6] [7] [8]
<i>Mazama sp.</i>	[1] [2] [3] [4]	[3] [7]
<i>Cuniculus paca</i>	[1] [2] [3] [4]	[3] [8] [9]
<i>Dasyprocta azarae</i>	[1] [3]	[3] [7]
* <i>Didelphis albiventris</i> or <i>D. marsupialis</i>	* <i>Didelphis albiventris</i> or <i>D. marsupialis</i>	* <i>Didelphis albiventris</i> or <i>D. marsupialis</i>

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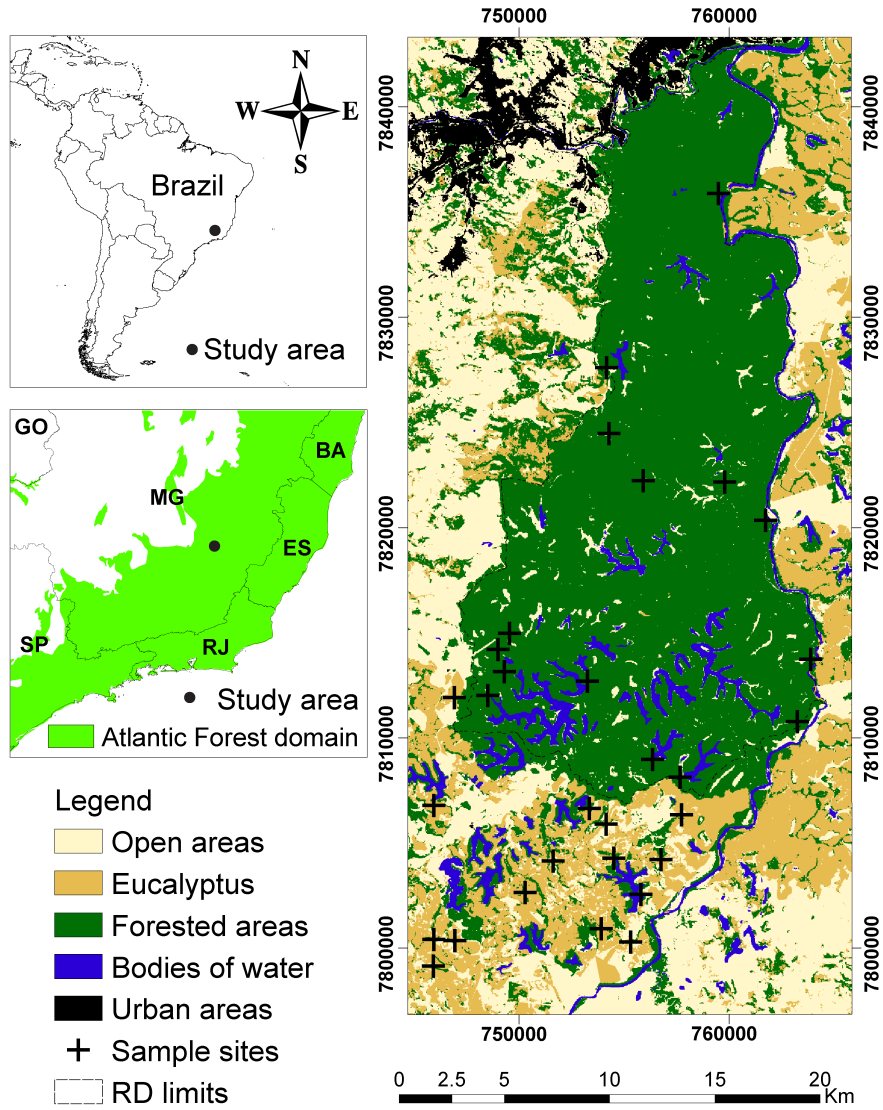
Appendix 2. Results of the Mardia-Watson-Wheeler test (W) used to compare the temporal activity of medium- to large-sized terrestrial mammals between the Rio Doce State Park and its adjacent areas of eucalyptus plantations, southeastern Brazil. Significant statistics ($P < 0.05$) indicate differences in the temporal activity pattern of the species between areas and, therefore, data were analyzed separated in these cases.

Species	W
<i>Panthera onca</i>	0.63
<i>Puma concolor</i>	6.45
<i>Leopardus pardalis</i>	9.32
<i>Cerdocyon thous</i>	*
<i>Eira barbara</i>	*
<i>Nasua nasua</i>	1.53
<i>Didelphis aurita</i>	1.97
<i>Tamandua tetradactyla</i>	*
<i>Priodontes maximus</i>	*
<i>Dasypus novemcinctus</i>	4.61
<i>Sylvilagus brasiliensis</i>	38.31

Species	<i>W</i>
<i>Tapirus terrestris</i>	11.90
<i>Pecari tajacu</i>	5.91
<i>Mazama</i> sp.	14.06
<i>Cuniculus paca</i>	*
<i>Dasyprocta azarae</i>	4.45
n <10 in at least one of the areas, which is below the minimum requirements for the statistical test	* n <10 in at least one

Appendix 3. Results of the Mardia-Watson-Wheeler tests, indicating whether or not the temporal activity overlap was significantly dissimilar ($P > 0.05$) between predators, and between predators and their prey in Rio Doce State Park (RD) and its adjacent areas of eucalyptus plantations (EP). “*W*” is the test statistics. The symbol “*” indicates that the species is not a potential prey for the predator, and “-” a relationship with no use for this study. The degrees of freedom used were 2 in all cases.

Species	Site	<i>P. onca</i>	<i>P. onca</i>	<i>P. concolor</i>	<i>P. concolor</i>	<i>P. concolor</i>	<i>P. concolor</i>	<i>L. pardalis</i>
		RD+EP <i>W</i>	RD+EP <i>P</i>	RD <i>W</i>	RD <i>P</i>	EP <i>W</i>	EP <i>P</i>	RD <i>W</i>
<i>Puma concolor</i>	RD	5.8	0.055					
<i>Puma concolor</i>	EP	11.1	0.004					
<i>Leopardus pardalis</i>	RD	3.3	0.190	4.7	0.098	-	-	
<i>Leopardus pardalis</i>	EP	0.4	0.836	-	-	17.9	0	
<i>Cerdocyon thous</i>	RD+EP	1.1	0.575	1.4	0.490	7.1	0.028	1.6
<i>Eira barbara</i>	RD+EP	23.2	0	31	0	6.1	0.047	29.8
<i>Nasua nasua</i>	RD+EP	26.6	0	33	0	3.8	0.152	43.1
<i>Didelphis aurita</i>	RD+EP	0.8	0.667	28.6	0	27	0	18.3
<i>Tamandua tetradactyla</i>	RD+EP	1.8	0.413	7	0.030	13.9	0.001	3.8
<i>Priodontes maximus</i>	RD+EP	3.5	0.173	*	*	*	*	*
<i>Dasyppus novemcinctus</i>	RD+EP	3.7	0.155	52.5	0	32.6	0	41.2
<i>Sylvilagus brasiliensis</i>	RD	11.8	0.003	15	0.001	-	-	14.5
<i>Sylvilagus brasiliensis</i>	EP	3.2	0.201	-	-	27	0	-
<i>Tapirus terrestris</i>	RD	3.1	0.216	*	*	*	*	*
<i>Tapirus terrestris</i>	EP	0.3	0.869	*	*	*	*	*
<i>Pecari tajacu</i>	RD	17.7	0	15.3	0	-	-	*
<i>Pecari tajacu</i>	EP	16	0	-	-	1.8	0.413	*
<i>Mazama</i> sp.	RD	0.1	0.935	4.4	0.110	-	-	*
<i>Mazama</i> sp.	EP	16	0	-	-	1.4	0.496	*
<i>Cuniculus paca</i>	RD+EP	0.6	0.748	4	0.137	13.2	0.001	3.1
<i>Dasyprocta azarae</i>	RD+EP	37.2	0	99.3	0	9.4	0.009	134



figures/Figure-2/Figure-2-eps-converted-to.pdf

figures/Figure-3/Figure-3-eps-converted-to.pdf