

RESEARCH ARTICLE

Influence of vegetation physiognomy, elevation and fire frequency on medium and large mammals in two protected areas of the Espinhaço Range

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ABSTRACT. The objectives of this study were to determine the richness of medium and large mammal species in two protected areas of the Espinhaço Mountain Range, state of Minas Gerais, Brazil; and to investigate the factors affecting the occurrence of those species. To accomplish that we placed 49 camera traps activated by heat and motion at Rio Preto State Park (RPSP) and 48 at Sempre Vivas National Park (SVNP). We also collected data on three environmental variables: vegetation physiognomy, elevation and wildfire frequency, to evaluate the influence of these factors on species richness and use intensity (inferred from camera trap detection rate) by large mammals. We recorded 23 large mammal species in the two parks combined. The lowest species richness was found at the rupestrian habitat of RPSP, and in the open grasslands of SVNP. The forest and savannah physiognomies were used more intensively by large mammals. Species richness was higher and use was greater at lower elevations of RPSP. In SVNP, fire frequency did not affect species richness or use intensity. The savannah habitat had very similar richness compared to the forests of the two protected areas. The high species richness and use intensity observed in these forest habitats highlights the importance of riparian environments in the Cerrado biome. The highest species richness and use intensity observed at low elevation follows patterns found in the literature, probably due to variation in the vegetation, which results in greater resource availability. Although rupestrian habitats at high elevations of the Espinhaço Range are known to have a high degree of endemism for some taxa, large mammal richness and use were not high in this habitat. These results indicate that the protection of native vegetation at lower elevations is crucial for the long-term conservation of large mammals in the Espinhaço Range.

KEY WORDS. Cerrado, campo rupestre, species richness, use of habitat, wildfire.

INTRODUCTION

Understanding which factors affect species richness is a challenge for ecologists. Resource availability in the ecosystem, the degree of specialization of species and the coexistence of species that share the same resources are key determinants of local species richness (MacArthur 1972). Generally, heterogeneous habitats provide the conditions for the establishment of a large number of species (Kerr and Packer 1997, Kreft and Jetz 2007, Stein et al. 2014). In fact, a review of studies on environmental heterogeneity and diversity found that 85% of the publications arrived at a positive correlation between heterogeneous ecosystems and species richness (Tews et al. 2004), including mammals (e.g., Southwell et al. 1999, Williams et al. 2002). Among the exceptions to this is the work of August (1983), who did not

find a positive relationship between habitat heterogeneity (as defined by the horizontal variation within a habitat) and mammal species richness in the Venezuelan llanos, even though habitat complexity (as defined by the vertical stratification of the habitat) in his data was positively correlated with richness.

Habitat heterogeneity also allows the coexistence of competitor species, therefore contributing to local species richness. For example, Schuette et al. (2013) observed that carnivore mammals in Africa responded in different ways to environmental factors, and noted that this variation could be responsible for the high local diversity of carnivores. Similarly, environmental heterogeneity is regarded as one of the main factors allowing the coexistence of two large Neotropical predators, the jaguar, *Panthera onca* (Linnaeus, 1758), and the puma, *Puma concolor* (Linnaeus, 1771) (Sollmann et al. 2012). To limit the negative

effects of competition on species' fitness, natural selection favors certain adaptations in morphology, behavior and natural history (Hardin 1960, Creel et al. 2001, Pfenning and Pfenning 2005). These adaptations are evident in several large terrestrial mammals, where differences in morphology (such as body mass) and ecology (diet, habitat selection and activity patterns) allow species coexistence and resource partitioning (Karanth and Sunquist 1995, Fedriani et al. 2000, Sinclair et al. 2003, Hayward and Slotow 2009, Oliveira-Santos et al. 2012, Macandza et al. 2012, Schuette et al. 2013, Ferregueti et al. 2015).

Several studies have investigated how biotic and abiotic features affect mammal distribution (e.g., Kinnaird and O'Brien 2012, Linkie et al. 2007, Sunarto et al. 2012). Likewise, habitat use in sympatric species is also frequently studied in tropical communities (e.g., Kinnaird and O'Brien 2012, Sollmann et al. 2012, Ahumada et al. 2013, Schuette et al. 2013). For example, Kinnaird and O'Brien (2012) found that environments with greater degrees of restriction on human activities favor the occurrence of medium and large mammals in Kenya. In Costa Rica, Ahumada et al. (2013) assessed how environmental factors such as altitude and canopy height influence the occurrence of mammals and found a variety of responses among the species evaluated. Sunarto et al. (2012) studied populations of tigers in Sumatra and showed that vegetation cover is essential for the presence of the species.

In the Brazilian Cerrado, gallery forests are known to play an important role in mammal distribution, as they provide unique resources within the ecosystem (Redford and Fonseca 1986, Johnson et al. 1999). Nevertheless, in a local or regional scale there is a lack of understanding about the environmental determinants of large mammal occurrence and species richness in the Cerrado. This biome is the second largest ecosystem in Brazil and is formed by a mosaic of grasslands, savannas and forests (Ribeiro and Walter 2008). Due to its large extension, contact with four major Brazilian ecosystems and environmental heterogeneity, the Cerrado harbors a large number of species (Silva et al. 2006), and is recognized as the most biodiverse savannah in the world (Klink and Machado 2005). Regarding mammals, 251 species have been recorded in this ecosystem (Paglia et al. 2012), of which 42 are medium and large species (body mass > 1 kg; Marinho-Filho et al. 2002).

Considering the high environmental heterogeneity found in the Cerrado and the relevance of protected areas for the conservation of large mammals, the objectives of this study were to determine large mammal species richness in two protected areas (PAs) of the Espinhaço Mountain Range and to investigate the factors affecting the occurrence of these species. We hypothesized that large mammal species richness and intensity of use would be higher in more complex habitats, in lower elevation, and in areas that are less frequently affected by fires.

MATERIAL AND METHODS

The Espinhaço Mountain Range is one of the most important Brazilian biogeographic regions. It extends over

parts of three major ecosystems: Caatinga, Cerrado and Atlantic Rainforest, the last two being recognized as global biodiversity hotspots (Myers et al. 2000, Mittermeier et al. 2005). This mountain range is one of the most important centers for species endemism in South America, with several new species of different taxonomic groups described recently (Azevedo and Silveira 2005, Oliveira and Sano 2009, Freitas et al. 2012, Barata et al. 2013, Pardiñas et al. 2014) and its biological relevance has been highlighted in prioritization studies for biodiversity conservation (e.g., Drummond et al. 2005, MMA 2007, Silva et al. 2008).

The Espinhaço Mosaic (Mosaico do Espinhaço: Alto Jequitinhonha-Serra do Cabral, as it is called in Portuguese) is composed of seven strict PAs (IUCN categories I–IV) and five multiple-use PAs (Area de Proteção Ambiental; IUCN category V) located in the southern portion of the Espinhaço Range. Most of this mosaic is within the Cerrado ecosystem, whereas the Atlantic Forest covers its eastern-most portion. Due to its irreplaceability, the Espinhaço Mosaic has been recognized as a priority area for conservation (Silva et al. 2008). This study focused on two strict PAs in this region: Rio Preto State Park (RPSP) and Sempre-Vivas National Park (SVNP).

Established in 1994, RPSP encompasses an area of 121 km² covered mostly by open vegetation such as 'campos rupestres' (rocky outcrops covered by scattered herbs, grasses and shrubs) and savannah, but also with gallery forests bordering water courses. There is a broad elevational gradient in the park, ranging from 750 to 1,800 m asl. Due to the fact that this reserve was established two decades ago, and that it is very effectively managed (WWF 2016), the impact of recent anthropogenic factors on the mammals that inhabit the area is assumed to be negligible.

Sempre-Vivas National Park was established in 2002 and covers an area of 1,241 km². The main vegetation physiognomies in SVNP are campos rupestres and open grasslands, but there are also portions of savannah, veredas (a humid grassland dominated by the palm species *Mauritia flexuosa* L. f.), dry forests and gallery forests. The elevation ranges from 650 to 1,525 m asl. However, due to SVNP's large area and logistical constraints, sampling was limited to between 1,000 and 1,400 m asl, including most of the park's vegetation physiognomies, but not veredas and dry forests normally associated with lower elevation. Within the limits of SVNP there are several land-use issues that result in anthropogenic impacts (such as poaching, wildfire and fuelwood collection). Wildfires are frequently detected in this PA (INPE 2015), but there is no reliable measure of poaching and fuelwood collection intensity inside the park. Both are certainly more intensive than at RPSP, but likely to be less common than in adjacent unprotected natural lands.

We used camera traps activated by heat and motion (Bushnell Trophycam) to study the large mammal community. The sampling design followed recommendations from Team Network (2008) and O'Brien (2010) with minor adaptations. Potential sampling sites (location where camera traps would be installed) were plotted at a density of 1 site per 2 km², representing a distance of 1.5 km between sites. At RPSP potential

sites were plotted throughout the entire park and in a small private reserve adjacent to the park, whereas in the much larger SPNP potential sites were established in the southern portion, with the park's lodge roughly in the centre.

In the field, we used a GPS unit to navigate to the potential sites and establish the camera trap within a 100 m radius from the predetermined location, choosing the spots with the highest probability of recording medium and large mammal species. Due to difficult access conditions, in four occasions at RPSP and in two occasions at SVNP camera trap were established out of the 100 m radius, but within a 250 m radius. Additionally, we had to relocate two potential sites at RPSP, because we were unable to reach them (e.g. cliffs). As a result, these two sites were established at a distance of 1.2 km of the nearest neighboring site.

In total we set up 51 camera trap sites at RPSP (including three sites at an adjacent private reserve) and 55 at SVNP, however, due to malfunctioning of some camera trap units, the final number of sites used in the analysis was 49 at RPSP and 48 at SVNP (Fig. 1). We conducted the surveys only during the dry season, from June–September 2013 at RPSP (average sampling days per site: 57.18, range: 7–108) and May–June 2014 at SVNP (average sampling days per sites: 39.75, range: 9–50). Surveys happened during the dry season to minimize camera malfunction from the accumulation of humidity inside the equipment. We assumed this would not have an important effect on our data since large Neotropical mammals do not perform long-distance seasonal migrations. Conducting camera trapping in the dry season has been adopted in several tropical regions of the world by the Team Network (2008). No lure was used to attract animals in either of the PAs.

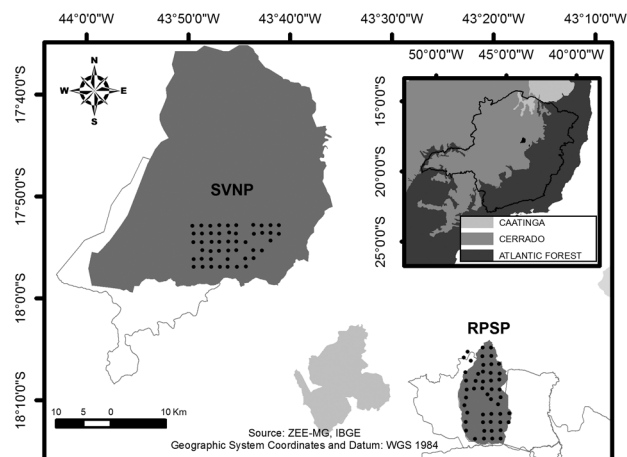


Figure 1. Camera trap sites (black circles) surveyed at Rio Preto State Park and Sempre Vivas National Park. Areas of integral protection in gray and areas of sustainable use in hollow polygons.

Considering our hypothesis, we collected data on three environmental variables: (1) vegetation physiognomy, (2) elevation and (3) wildfire intensity. Physiognomy was assigned to

four possible categories: forest (gallery forest or capão forest), savannah (small trees and shrubs with a herbaceous layer), open grassland (with or without scattered trees) and rupestrian habitat (campos rupestres or rock outcrops with scattered vegetation). Elevation was measured in the field using a GPS unit. Wildfire frequency was extracted from a Kernel Map provided by PA management team, which was produced using data available from INPE (2015) on heat spots density within the limits of SVNP, between 1999 and 2012. In this map, the pixel value of the camera trap site was used as a covariate, where smaller values indicated low fire frequency and larger values indicated high fire frequency. We used ArcGIS 10 to produce the map and to extract values for the analysis.

We built a matrix of independent camera trap records of large mammals for each PA. When there were two records of the same species in a single sampling site we assumed them to be independent if the observations were at least 24hs apart. We used the software EstimateS 9.1.0 (Cowell 2013) to randomize the sampling and obtain all species richness estimates presented here. To be able to compare species richness between the two parks, we applied the rarefaction function to data from SVNP, as it had a smaller sampling effort than RPSP. The parameter “S(Est)”, which represents the average number of recorded species as a function of sampling effort, and its 95% CI were used to build species accumulation curves for each park.

To assess the effect of the Cerrado physiognomies on species richness, we grouped the records from each vegetation physiognomy (forest, savannah, grassland, rupestrian). Since there were large differences in sampling effort between physiognomies, the rarefaction function provided estimates with very broad CIs. For this reason, we decided to perform the comparison, controlling for the physiognomy with the smallest sampling effort (forest in both parks). Therefore, we obtained the average species richness in each physiognomy based on 452 and 420 sampling days/physiognomy at RPSP and SVNP, respectively. We checked for overlap between the 95% CI for each estimate to infer statistical significance. Additionally, as an overall measure of large mammal use, we grouped the independent records from all large mammal species within a physiognomy (overall photographic rate) and compared them through an analysis of variance (ANOVA). Although we cannot consider the overall photographic rate as a measure of abundance, we used this rate as a measure of the intensity of use by large mammals, in which a large number of independent records represents high use intensity of a given area. This analysis was performed for each park independently.

The effect of elevation on species richness was only assessed for RPSP, since the elevation variation of the sampling sites at SVNP only ranged from 1,041 to 1,369 m asl. In RPSP the difference between the lowest and highest sampling site was almost 1,000 m (range: 800–1,720 m asl). Following a well-established classification used by the park's management team, we divided the RPSP into two regions according to elevation: below 1,000 m asl and above 1,200 m asl. This division reflects

markedly different environments, where low elevation sites are dominated by savannah and forest habitats and high elevation sites are normally located in grasslands or rupestrian habitats. We thus grouped data from all sites at low (<1,000 m) and high elevation (>1,200 m), eliminating those sites established between 1,000–1,200 m asl. Species richness estimates with 95% CI was obtained for each region controlling for differences in sampling effort. To evaluate the intensity of use by large mammals we grouped the independent records from all species in low and high altitudes and compared them through independent T-tests.

Finally, we used linear regression to assess the effect of wildfire frequency on species richness and use intensity (defined as average records of all species of medium and large mammals) at SVNP. We excluded RPSP from this analysis because wildfires are rare in this park and there have been no occurrences of it in at least the last five years. To represent wildfire frequency in the sampling site, we extracted the value derived from the Kernel Map (see Data collection) for the pixel where the camera trap had been set. The average species richness and use intensity at the site level, controlling for differences in sampling effort, were obtained for all sites surveyed for more than 30 days at SVNP.

RESULTS

We recorded 23 large mammal species in the two parks combined, 19 at RPSP after 2,865 sampling days and 18 at SVNP after 2,010 sampling days (Table 1). Observed species richness was very similar among parks, with almost a complete overlap of estimates (Fig. 2). Despite the similarity in species richness, five species were recorded exclusively in RPSP: naked-tailed armadillo, *Cabassous* sp.; crab-eating fox, *Cerdocyon thous* (Linnaeus, 1766); puma, *P. concolor*; crab-eating raccoon, *Procyon cancrivorus* (G.[Baron] Cuvier, 1798); and agouti, *Dasyprocta* sp.; and four exclusively in SVNP: lowland tapir, *Tapirus terrestris* (Linnaeus, 1758); hoary-fox, *Lycalopex vetulus* (Lund, 1842); collared peccary, *Pecari tajacu* (Linnaeus, 1758); and capybara, *Hydrochoerus hydrochaeris* (Linnaeus, 1766).

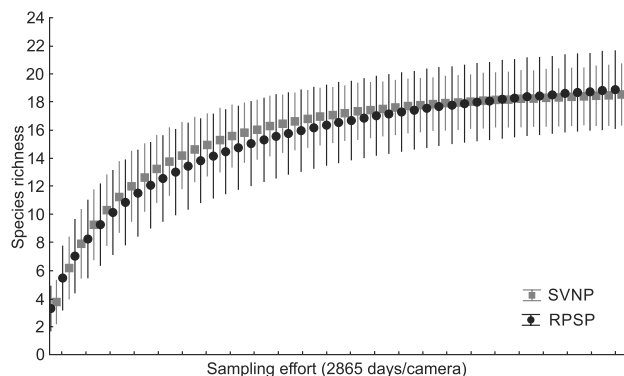
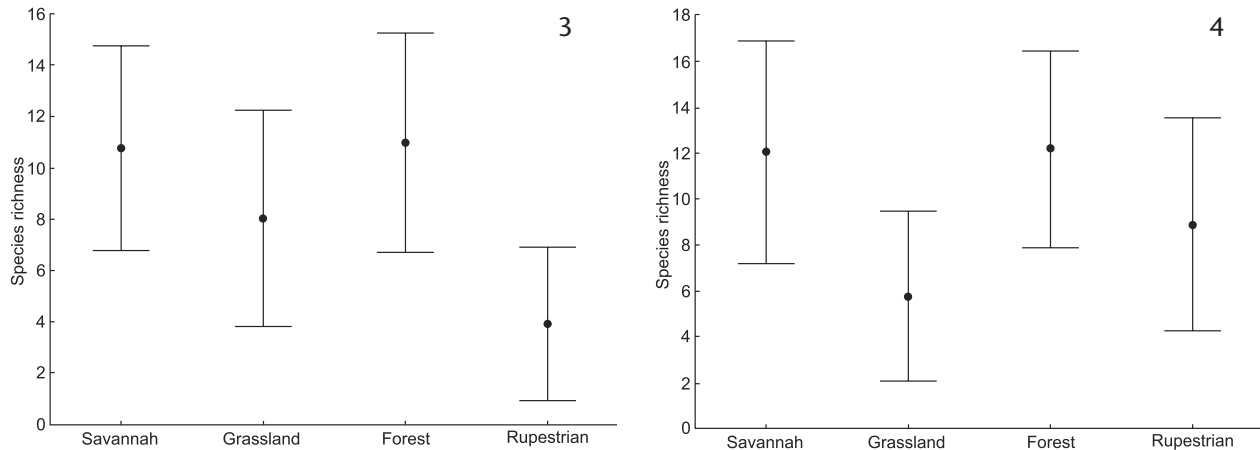


Figure 2. Species accumulation curve (richness x effort) and confidence interval (95%) in Rio Preto State Park (RPSP) and Sempre Vivas National Park (SVNP).

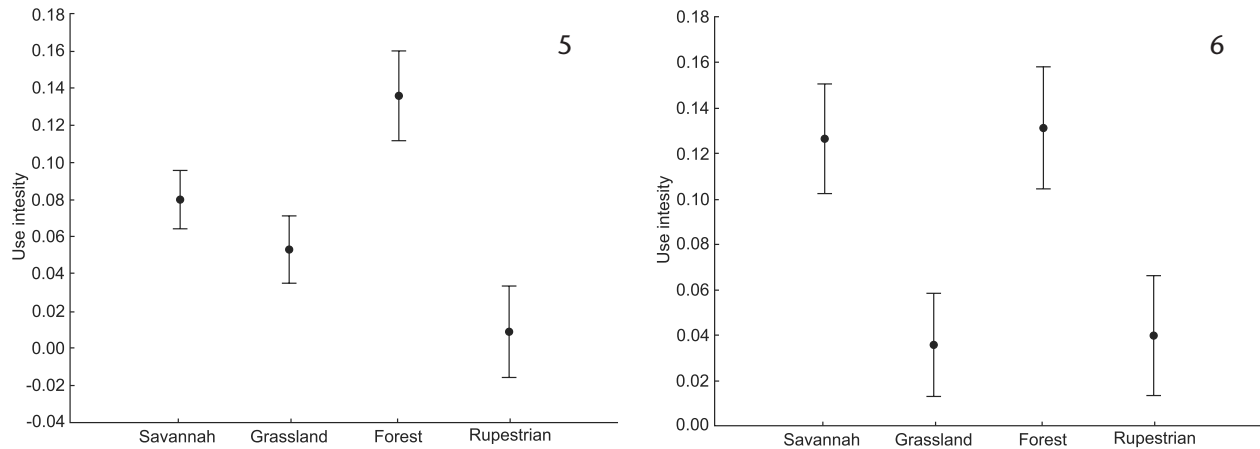
Table 1. Mammal species recorded at Rio Preto State Park (RPSP) and Sempre Vivas National Park (SVNP).

Taxonomic group	Popular name	RPSP	SVNP
Pilosa			
Myrmecophagidae			
<i>Tamandua tetradactyla</i> (Linnaeus, 1758)	Southern-anteater	x	x
<i>Myrmecophaga tridactyla</i> Linnaeus, 1758	Giant-anteater	x	x
Cingulata			
Dasypodidae			
<i>Dasyus</i> sp.	Armadillo	x	x
<i>Cabassous unicinctus</i> (Linnaeus, 1758)	Naked-tailed armadillo	x	
<i>Euphractus sexcinctus</i> (Linnaeus, 1758)	Yellow-armadillo	x	x
<i>Priodontes maximus</i> (Kerr, 1792)	Giant-armadillo	x	x
Carnivora			
Canidae			
<i>Cerdocyon thous</i> (Linnaeus, 1766)	Crab-eating fox	x	
<i>Chrysocyon brachyurus</i> (Illiger, 1815)	Maned-wolf	x	x
<i>Lycalopex vetulus</i> (Lund, 1842)	Hoary-fox		x
Mephitidae			
<i>Conepatus semistriatus</i> (Boddaert, 1785)	Striped hog-nosed skunk	x	x
Mustelidae			
<i>Eira barbara</i> (Linnaeus, 1758)	Tayra	x	x
Felidae			
<i>Puma yagouaroundi</i> (É. Geoffroy, 1803)	Jaguarundi	x	x
<i>Leopardus pardalis</i> (Linnaeus, 1758)	Ocelot	x	x
<i>Leopardus tigrinus</i> (Schreber, 1775)	Oncilla	x	x
<i>Puma concolor</i> (Linnaeus, 1771)	Puma	x	
Procionidae			
<i>Procyon cancrivorus</i> (G. Cuvier, 1798)	Crab-eating raccoon	x	
<i>Nasua nasua</i> (Linnaeus, 1766)	Coati	x	x
Perissodactyla			
Tapiridae			
<i>Tapirus terrestris</i> (Linnaeus, 1758)	Tapir		x
Artiodactyla			
Cervidae			
<i>Mazama gouazoubira</i> (G. Fischer, 1814)	Gray-brocket	x	x
Tayassuidae			
<i>Pecari tajacu</i> (Linnaeus, 1758)	Collared-peccary		x
Rodentia			
Cuniculidae			
<i>Cuniculus paca</i> (Linnaeus, 1766)	Spotted-paca	x	x
Dasyproctidae			
<i>Dasyprocta</i> sp.	Agouti	x	
Caviidae			
<i>Hydrochoerus hydrochaeris</i> (Linnaeus, 1766)	Capybara		x

The observed species richness was statistically lower in rupestrian habitats than other vegetation physiognomies in RPSP (Fig. 3) and in SVNP the species richness in grassland was statistically lower than forest and savannah (Fig. 4). The use intensity (records rate of all species grouped) showed significant variation among physiognomies (RPSP: $F_{3,2819} = 18.9$, $p < 0.001$; SVNP: $F_{3,1959} = 17.3$, $p < 0.001$). The forest in RPSP was clearly the most intensively used habitat, whereas the rupestrian habitat had a very low level of use (Fig. 5). Similarly, forest in SVNP, was the most frequently used habitat (although the savannah showed similar levels), while the grasslands and rupestrian habitats had much lower use intensity (Fig. 6).



Figures 3–4. Observed species richness and confidence interval (95%) by physiognomy in (3) Rio Preto State Park and (4) Sempre Vivas National Park.



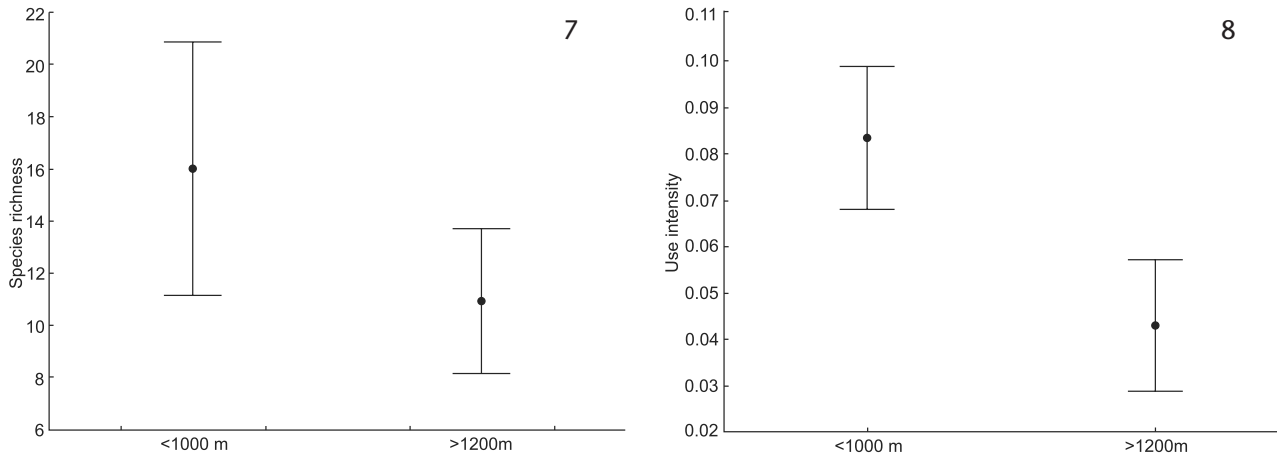
Figures 5–6. Medium and large mammals use intensity and confidence interval (95%) by physiognomy in (5) Rio Preto State Park and (6) Sempre Vivas National Park.

At lower elevations, species richness (Fig. 7) and use intensity ($F_{(2,178)} = 3.79$, $p < 0.001$) (Fig. 8) were statistically higher in RPSP. The wildfire frequency did not show a significant effect on species richness ($R_{(1, 38)} = 0.073$, $p = 0.65$) or use intensity ($R_{(1, 38)} = 0.13$, $p = 0.43$) in SVNP.

DISCUSSION

Total species richness recorded here represents 70% and 55% of all large mammals known to occur at the Espinhaço Range (Lessa et al. 2008) and the Brazilian Cerrado (Marinho-Filho et al. 2002), respectively. While the trend of species accumulation curves' to stabilize indicates that a large proportion of the target community has been recorded, some species known to occur in these parks were not detected. For instance, the Neotropical otter, *Lontra longicaudis* (Olfers, 1818), and the lesser grison, *Galictis cuja* (Molina, 1782)

have been recorded in RPSP (Lessa et al. 2008), whereas *P. concolor* and *P. onca* have been recently recorded by camera traps in SVNP (Instituto Biotropicos Archive). Considering these four species and the species we recorded in this study, RPSP and SVNP together harbor virtually all large mammal species known to currently occur in the Espinhaço Range. The presence of some species recorded exclusively in one of the parks (such as puma and crab-eating raccoon in RPSP or capybara in SVNP) can be explained by the relatively short duration of the surveys. Nevertheless, unpublished data from RPSP and information from experienced park rangers suggest that the tapir and the collared peccary are likely restricted to SVNP. Poachers frequently target these two species, and therefore their numbers may decline in the presence of anthropogenic pressure (Cullen-Jr et al. 2000). It is possible that they have become locally extinct at RPSP (which is smaller and easier to access than SVNP) before the PA was established.



Figures 7–8. (7) Species richness and confidence interval (95%) in low (<1000 m) and high elevation (>1200 m) in Rio Preto State Park. (8) Use intensity by medium and large mammals and confidence interval (95%) in low (<1000 m) and high elevation (>1200 m) in Rio Preto State Park.

The high species richness and use intensity observed in forest habitats highlight the importance of riparian environments in the Cerrado, which may provide essential resources for mammals, especially during the dry season (Johnson et al. 1999, Redford and Fonseca 1986). Forest habitats cover less than 10% of the study areas, but a large proportion of total species richness, 58 and 67% in RPSP and SVNP, respectively, occurred in forests. Higher large mammal species richness in forest environments was also observed in another PA in the Espinhaço Range (Serra do Cipó National Park; Oliveira et al. 2009). As these habitats are associated with watercourses in the region, we can infer that at least part of the home range of most large mammal species must encompass forest habitats.

The species richness in savannah and forest habitats was very similar in the two PAs studied. Some studies show that the mammal community of riparian forests appears to be more similar to the savannah than to any other physiognomy of the Cerrado (Alho et al. 1986, Johnson et al. 1999). Although the composition varied between these two habitats in each PA, only one species – the southern anteater, *Tamandua tetradactyla* (Linnaeus, 1758) – had been registered in the savannah and not in the forest, whereas all the species registered in the forest were also found in the savannah. Grasslands also represented an important part of the richness found in the two PAs (11 in RPSP and 7 in SVNP), with a total of 15 species registered in this vegetation physiognomy. This species richness is higher than the richness of medium and large mammals found by Oliveira et al. (2009) in the open areas of Serra do Cipó National Park.

The species richness found in rupestrian habitats of RPSP was much lower than in the other vegetation physiognomies, whereas in SVNP species richness in this habitat was reasonably high – higher than in the grasslands and not varying significantly in relation to forest and savannah. This variation may be due

to the specific characteristics of the PAs. Due to the greater elevational gradient of RPSP the rupestrian environments in this park are, in general, steeper, which can make it difficult for the animals to move. In SVNP the elevational variation between rupestrian environments and other vegetation physiognomies are milder and less steep (at least in the survey area), facilitating displacement in these environments in the PA. The variations in species richness between physiognomies (especially in RPSP) could be attributed to differences in productivity, habitat complexity, and protection against predators among them. Areas that are more productive tend to have higher species richness (Waide et al. 1999, Jetz et al. 2009, Sandomet al. 2013), which could explain the lower species richness in the rupestrian habitat, a less productive environment due to its soil characteristics (Rodela 1998). The majority of the species recorded in this environment probably only use it occasionally, since it is difficult to maneuver in it and there are few resources and shelter for large animals.

The frequency of records between physiognomies indicated clear variations in the use of different environments. The high amount of records in forests suggests that these environments are more intensely used by wild mammals. Forest habitats play an important role in mammal diversity in the Cerrado, as they provide refuge for several species and, generally, have more food and water available (Redford and Fonseca 1986). August (1983) pointed out that forest habitats provide a variety of food types that are rarely available in other habitats. It is important to highlight that, although the two PAs are dominated by rupestrian habitats, the rate of independent records in this environment was almost always lower than those of the forest and savannah physiognomies. To our knowledge, no study has evaluated the use of rupestrian habitats by medium and large sized mammals. Although several studies have been carried out in PAs that have

this predominant vegetation physiognomy, in many cases (e.g., Leal et al. 2008, Lessa et al. 2008, Oliveira et al. 2009), the use of this environment by large mammals has not been evaluated.

The higher species richness and intensity of use in lower elevations was expected. The decline in richness due to increasing elevation is widely accepted as a general standard (Rahbek 1995, 2005). Rahbek (1995) highlighted two main models of species distribution along elevational gradients: (1) the monotonic model, in which there is a linear decrease in the number of species with increasing altitude, observed in plants (Stevens 1992), bats (Patterson et al. 1996) and birds (Terborgh 1971, 1977, Rahbek 1997) and (2) the dome-shaped model, with higher species richness in the intermediate ranges of the elevation gradient, observed in non-flying mammals (Geise et al. 2004), insects (Mccoy 1990, Fleishman et al. 1998) and birds (Rajão and Cerqueira 2006).

Although the maximum elevation of RPSP (not exceeding 2,000 m) is insufficient for direct effects on the medium and large mammal fauna, it is certainly sufficient to change the vegetation structure and can thus indirectly influence their distribution. The elevational gradient has traditionally been used as a substitute for productivity, with the assumption that at higher elevation the environmental conditions contribute to lower productivity (MacArthur 1969, Terborgh 1971, Navarro 1992, Lee et al. 2004, Rahbek 2005). In fact, in RPSP, the more complex and productive habitats are in the lower part of the PA, where there are riparian forests along the Preto River (and other streams) and savannah areas with denser vegetation cover. These features may act as an indirect variable on the composition of medium and large mammals. The upper part of the park has a large area of rupestrian habitats and grasslands, with just a few forest patches that have a more abrupt transition to open vegetation, minimizing the productivity and niche availability and consequently species richness. The area of open grasslands in the upper part of RPSP is unfavorable to the determining factors of species richness, such as complexity (August 1983), habitat heterogeneity (Southwell et al. 1999, Williamset al. 2002) and primary productivity (Waide et al. 1999, Jetz et al. 2009, Sandomet al. 2013).

The absence of effects of wildfire frequency on species richness and use intensity is likely a result of the adaptation of Cerrado plant species to this characteristic of the biome. Felfili et al. (2000) pointed out that the Cerrado is highly fire resilient due to the characteristics of the vegetation, which prevent high mortality of trees and a rapid regrowth of the herbaceous layer in those situations. Although the immediate effect of a fire is a drastic change in the landscape, the mobility of medium and large mammals would allow most of them to escape and seek refuge in adjacent areas (Frizzo et al. 2011). In these cases, gallery forests are important refuge areas for these species (Silveira et al. 1999, Prada and Marinho-Filho 2004). Due to the rapid regrowth of the vegetation, soon after the fire, these highly resilient environments may be able to sustain populations of medium and large mammals again.

Two main aspects need to be considered in order to understand the influence of fire on the fauna: frequency and intensity. Infrequent fires result in a large accumulation of biomass. When the area eventually catches on fire, it is much more intense, with larger flames, higher temperatures and lasts longer (Miranda et al. 1993). This type of fire can have catastrophic effects on the local fauna (Ramos-Neto and Pivello 2000). At Emas National Park, Silveira et al. (1999) observed that a high-intensity fire caused negative effects on mammal populations. A second fire, in the following year with less biomass to burn, was less intense, and its effects were reduced. The recent history of annual fires at SVNP will likely result in less intense future fires and may minimize the impacts on the mammal fauna.

Even though the Espinhaço range is recognized as an important center for species endemism in Brazil (Silva and Bates 2002, Simon and Proença 2000), only 2.6% of its area is covered by strict PAs (Silva et al. 2008). Additionally, only a small portion of these areas is large enough (>500 km²) to safeguard relevant populations of large mammal species (Chiarello 2000a, b). In fact, many of the PAs in the Brazilian Cerrado are not effectively managed and are suffering from moderate or high anthropogenic pressure (WWF-Brazil and ICMBio 2012), which can result in local extinctions.

A global analysis revealed that PAs networks are generally established on higher elevations, steeper slopes and greater distance from urban centers, limiting their ability to avoid natural habitat conversion (Joppa and Pfaff 2009). This is true for the great majority of PAs in the Espinhaço Range, which are located at higher elevations and on steeper slopes. Nevertheless, in this specific case, the bias is biologically reasonable due to the large number of endemic species in rupestrian habitats, a habitat associated with higher elevations in this mountain range (e.g., Azevedo and Silveira 2005, Oliveira and Sano 2009, Freitas et al. 2012, Barata et al. 2013, Pardiñas et al. 2014). Our data, however, showed that this habitat does not seem to be relevant for the large mammal community in the Espinhaço. In fact, we observed higher levels of large mammal diversity in habitats usually found in lower elevations, forest and savannah. Therefore, the protection of native vegetation at lower elevations is crucial for long-term large mammal conservation in the Espinhaço Range. This could be achieved with strategic expansion of the PA network, as well as through the establishment of biodiversity corridors using riparian forests to connect existing PAs. The establishment of new PAs in the Espinhaço Range has been recommended before, as the present size of the PAs is considered insufficient to promote mammal conservation (Rocha et al. 2005).

In this study we found that the evaluated PAs are home to a significant portion of the known medium and large mammals of the Espinhaço Range. The SVNP, however, is one of the PAs of the Espinhaço that still suffers from anthropogenic pressures. Because this national park is the largest PA in the Espinhaço Mosaic and the second largest in the Espinhaço Range, it is

essential to eliminate these pressures in order to maintain the high diversity of mammals in the region. In recent years some groups have joined efforts for the re-categorization (downgrading) of SVNP from a strict PA to a multiple-use PA. From a conservation point of view, this would be a major setback for the biodiversity of the Espinhaço Range and we emphasize that priority must be given to effective regulation and implementation of the strict PAs for the conservation of numerous threatened species.

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