Cerrado Mammals in Secondary Savanna

Assessing the Conservation Value of Secondary Savanna for Large Mammals in the Brazilian Cerrado

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Received:___________; Revision accepted:___________.

ABSTRACT

Debate about the conservation value of secondary habitats has tended to focus on tropical forests, increasingly recognizing the role of secondary forests for biodiversity conservation. However, there remains a lack of information about the conservation value of secondary savannas. Here, we conducted a camera trap survey to assess the effect of secondary vegetation on large mammals in a Brazilian Cerrado protected area, using a single season occupancy framework to investigate the response of individual species (species-level models) and of all species combined (community-level models). Additionally, we investigated the cost-effectiveness of different sampling designs to monitor globally threatened species in the study area. For community-level models there was moderate support for the effect of succession stage on occupancy; though secondary areas that regenerated from eucalyptus plantation had similar community occupancy estimate as old growth areas. Species-level models showed little support for the effect of succession on occupancy of the ten species assessed. Our results demonstrate that secondary vegetation does not appear to negatively impact large mammals in the study area and suggest that, given a favourable context, Cerrado mammals can recolonize and use secondary habitats that regenerated from clear cut. However, our study area should be considered a best-case scenario, as it retained key ecological attributes associated with high-value secondary habitat. Our simulations showed that a sampling design with 60 camera trap sites surveyed during nine occasions is appropriate to monitor most globally threatened species in the study area, and could be a useful starting point for new monitoring initiatives in other Cerrado areas.

RESUMO

O debate sobre a importância de habitats secundários para a conservação tende a focar em florestas tropicais, existindo evidência considerável sobre o papel das florestas secundárias na manutenção da biodiversidade. Entretanto, praticamente não existe informação sobre a importância de savanas secundárias para a conservação. Neste trabalho utilizamos registros de armadilhas fotográficas e modelos de ocupação para avaliar o efeito da vegetação secundária sobre mamíferos de médio e grande porte em uma unidade de conservação do Cerrado. Investigamos também a relação custo-benefício de diferentes desenhos amostrais para monitorar espécies globalmente ameaçadas de extinção na área de estudo. Para os modelos de comunidade houve suporte moderado para o efeito do estágio sucessional sobre a ocupação, apesar de que áreas secundárias que regeneraram de plantio de eucalipto tiveram estimativa similar às áreas primárias. Para os modelos de espécies houve pouco suporte para o efeito do estágio sucessional sobre a estimativa de ocupação das 10 espécies avaliadas. Nossos resultados mostram que aparentemente a vegetação secundária não afeta de forma negativa os mamíferos de médio e grande porte na área de estudo. Além disso, os resultados sugerem que, em um contexto favorável, mamíferos do Cerrado podem recolonizar e usar habitats secundários que regeneraram após o corte raso. Entretanto, nossa área de estudo deve ser considerada como uma situação ideal, já que os habitats secundários nela encontrados possuem características de ambientes com alto valor para conservação. Nossas simulações mostraram que um desenho amostral com 60 pontos de armadilhas fotográficas amostrados durante nove ocasiões é apropriado para monitorar a maioria das espécies globalmente ameaçadas presentes na área de estudo, e pode ser um ponto de partida para novas iniciativas de monitoramento em outras áreas do Cerrado.

Keywords: camera trap; Minas Gerais; occupancy analysis; secondary vegetation

THE AREA OF THE PLANET COVERED BY SECONDARY VEGETATION IS PREDICTED TO INCREASE BY between 35-75% by 2100, resulting in a large decrease in primary habitat (Hurtt *et al.* 2011). Given such projected changes, secondary habitats will become an essential element of longer-term conservation strategies. Currently, most of the debate about the conservation value of secondary habitats has focused on tropical forests (*e.g.* Chazdon *et al.* 2009; Gibson *et al.* 2011), with a great deal of research supporting the role of secondary forests in the maintenance of tropical forest biodiversity in the face of growing threats (Barlow *et al.* 2007, Chazdon *et al.* 2009, Dent & Wright 2009, Solar *et al.* 2015 - though see Gibson *et al.*(2011) on the irreplaceability of primary forests).

Despite the research interest in primary and secondary forests, there remains a lack of information about the conservation value of secondary savannas, and far less attention has been devoted to such habitats. Even the definition of secondary savanna is not straightforward. Some authors (*e.g.* Backéus 1992, Barger *et al.* 2002) have adopted the term as a synonym of derived savanna, using it to describe secondary vegetation established after the destruction of a forest ecosystem. We adopt the suggestion from Veldman *et al.* (2015) and use the term "secondary savanna" to characterize a savanna vegetation that regenerated in a region that historically supported savanna ecosystems.

Cerrado, the Brazilian savanna, is formed by a wide variety of vegetation physiognomies encompassing grassland, savanna and forest formations (Felfili et al 2004; Ribeiro & Walter 2008), but the most widespread physiognomy consists of a savanna composed by trees and large shrubs about 2-8 m tall generating 10-60% cover, with a grass layer in the ground level (Ratter *et al.* 1997). In general the grass layer tends to decrease as the tree and shrub cover increases, and the balance between these two components of the vegetation depends on fire frequency, soil fertility and precipitation levels (Durigan & Ratter 2006, Veldman *et al.* 2015). Cerrado originally covered around 25% of the country (IBGE 2004) before wide-scale conversion to anthropogenic land uses. Official estimates indicate that approximately 50% of the ecosystem has already been converted (MMA 2014). Expansion of farmland is the main driver of habitat loss in Brazilian ecosystems (Lapola *et al.* 2013), and this threat is even more acute in the Cerrado, where 40% of the Brazilian agricultural Gross Domestic Product is produced (MMA 2014). In spite of its importance to the agricultural industry, some converted land may be abandoned or set aside, which could have important implications for persistence of wildlife. This land abandonment can occur for a variety of reasons, including economic changes that make an agricultural activity financially inviable or adjustment to legislation where a portion of the property must be set aside for environmental purposes.

Since most Cerrado vegetation physiognomies are, to some extent, capable of natural regeneration (Hoffmann 1999, Sampaio *et al.* 2007, Abreu *et al.* 2011), abandoned lands may recover to form secondary vegetation given time. For example, Jepson (2005) studied land cover dynamics in central Brazil Cerrado, and found that half of the land converted between 1986 and 1999 (*ca.* 670 km^2) regenerated into secondary native vegetation. However, secondary vegetation is structurally, floristically and functionally different from the original old growth vegetation (Whitfeld *et al.* 2014, Pezzini *et al.* 2014, Gomes & Maillard 2015).

Cerrado regeneration generally follows a path from open to dense vegetation, with regeneration typified by an increase in tree density and height, and a decrease in herbaceous cover (Durigan & Ratter 2006, Maillard & Costa-Pereira 2010). However, other factors such as frequency of fire and soil conditions also influence the characteristics of the late-succession stage, which can even support a well-developed grass layer (Veldman *et al.* 2015). Differences in habitat structure and plant community composition between secondary and old growth vegetation could influence spatial distribution and abundance of local fauna. For example, species that rely on the grassy layer for food or shelter may respond positively to an increase in the amount of secondary savanna in the landscape, especially in early regeneration stages. On the other hand, frugivorous animals could be negatively affected, as zoochoric plant species are replaced by those with abiotic dispersion syndrome in open Cerrado formations (Kuhlmann & Ribeiro 2016). These impacts on herbivores could subsequently influence higher trophic levels, ultimately affecting the whole animal community in the area.

Besides avoiding habitat conversion (Naughton-Treves *et al.* 2005, Carranza *et al.* 2014), protected areas may also promote vegetation recovery on abandoned lands, as anthropogenic impacts are reduced and natural succession is likely to happen. These observations are borne out in the case of Veredas do Peruaçu State Park (VPSP), a protected area in the Cerrado where roughly one third of the area is secondary vegetation that regenerated after clear cut (Gomes & Maillard 2015). VPSP harbours a rich large mammal fauna, comprising at least 28 species >1kg, including globally threatened and rare species (Ferreira *et al.* 2011, 2015). These facets make the protected area an excellent location for studying the impact of secondary vegetation on mammal abundance and distribution.

Here, we use a quasi-experimental design in order to assess the effect of secondary vegetation on large mammal occupancy (interpreted as probability of use; Mackenzie *et al.* 2004).

Since species with different ecological requirements may respond in different ways to vegetation change, we predicted that:

(1) occupancy of species with wide dietary breadth (such as yellow armadillo *Euphractus sexcinctus*, maned wolf *Chrysocyon brachyurus* and puma *Puma concolor*) would not be affected by succession stage because they could shift their diets to adapt to variation in resources (*e.g.* Dalponte & Tavares-Filho 2004, Jacomo *et al.* 2004, Moreno *et al.* 2006).

(2) occupancy would be lower in secondary savanna for species that have fruits as an important part of the diet (such as Azara's agouti *Dasyprocta azarae*, white-lipped peccary *Tayassu pecari* and lowland tapir *Tapirus terrestris*), due to a decrease in zoochoric trees and shrubs (Kuhlmann & Ribeiro 2016) and because larger (thus, older) plants generally produce more seeds and fruits (Chapman *et al.* 1992, Greene & Johnson 1994, Zardo & Henriques 2011).

(3) occupancy would be higher in secondary savanna for herbivores that feed predominantly on the grass layer and for species that favour more open habitats (such as Pampas deer *Ozotoceros bezoarticus* and giant anteater *Myrmecophaga tridactyla*), as secondary vegetation in VPSP tend to have a more open canopy (Gomes & Maillard 2015).

Though individual species may respond differently, we predicted community occupancy (a measure of overall use by large mammals) to be higher in old growth savanna for two reasons: 1) denser savanna formations tend to have higher net primary productivity (Grace *et al.* 2006, Pontes 2010); and 2) few species that potentially occur in VPSP (*ca.* 10%) have the ecological characteristics to greatly benefit from secondary vegetation. Additionally, due to a lack of specific recommendations on occupancy study design for Brazilian mammals and also to inform the establishment of cost-effective monitoring strategies in the Cerrado, we explored the effect of different sampling schemes on the precision of occupancy estimates for the globally threatened species recorded.

MATERIALS AND METHODS

STUDY AREA.—We conducted the study at Veredas do Peruaçu State Park, Minas Gerais state, south-eastern Brazil. The 310 km^2 state park protects part of the upper Peruaçu River watershed, a priority area for conservation in Brazil (MMA/PROBIO 2007) embedded in the Cerrado hotspot (Myers *et al.* 2000) (Fig.1).

VPSP is predominantly covered with savanna vegetation (cerrado *stricto sensu* covering approximately 95% of the area; WWF-Brasil 2014), generally presenting a fairly dense woody layer (Maillard & Costa-Pereira 2010). Vereda – a humid grassland dominated by the palm species *Mauritia flexuosa* – is also an important vegetation type occurring along the Peruaçu River and is concentrated in the park's northern and north-western limits. The Peruaçu River, and associated lakes, is virtually the only source of water inside VPSP during the dry season. The topography at VPSP is relatively flat (700 to 850 m asl) and the climate is highly seasonal, with a dry season from April to mid-October and a wet season from mid-October to March.

Before being legally protected in 1994, the area was used mainly for eucalyptus plantations, and, to a lesser extent, for charcoal production from native trees and cattle ranching. A single company was responsible for the eucalyptus plantation, which took place from late 1970s to the beginning of 1990s in more than 1/3 of the park's area (*ca*. 130 km^2) and involved the clear cut of the native vegetation (Gomes & Maillard 2015). The remainder of the company`s land was kept in its natural state with little or none direct human interference over the vegetation during the period of eucalyptus production, resulting in maintenance of old growth vegetation.

Charcoal production from native trees and cattle ranching occurred diffusely in smaller properties around the eucalyptus company land, but was more frequent in the southern portion of VPSP. It is not possible to accurately determine whether only one of these two activities happened in a specific location, but it is likely that a mix of both occurred frequently, with first most of the woody vegetation being removed for charcoal and then cattle being brought to browse on the herbaceous layer, with regular use of fire. For this reason, we classified these areas as mixed-use. Scattered and small patches of less disturbed savanna may have remained within these areas.

Savanna areas used for eucalyptus plantation in the past have a more open canopy, shorter trees, smaller basal area and slightly less trees and shrubs per hectare than old growth savanna (Maillard & Costa-Pereira 2010; Gomes & Maillard 2015), whereas the variation in vegetation structure within former eucalyptus areas is subtle and is likely to be better explained by fire history and other local conditions than regeneration age (Maillard & Costa-Pereira 2010). We did not have accurate information on vegetation structure of mixed-use areas, however, a lower NDVI value in portions of southern VPSP (Gomes 2006) and the general appearance of the vegetation allow us to infer that vegetation structure in sites that we classified as mixed-use is more similar to areas used for eucalyptus. Despite the difference in vegetation structure between secondary and old-growth savannas, both of them fall within a single Cerrado physiognomy (cerrado *stricto sensu*; WWF-Brasil 2014).

With protected area establishment in 1994, all the economic activity in the area finished and the savanna vegetation left to naturally regenerate. The age of secondary vegetation is not homogenous throughout the study area, as eucalyptus trees were logged in different years (Maillard & Costa-Pereira 2010). At the inception of our study, the youngest secondary vegetation in VPSP had been regenerating for 16 years and the oldest for 28 years.

DATA COLLECTION.—We surveyed 50 sampling sites (Fig. 1) with camera traps (Bushnell Trophycam) following a sampling design that has been widely adopted to estimate large mammal occupancy in different regions of the world (*e.g.* Ahumada *et al.* 2011, Kinnaird & O'brien 2012, Rovero *et al.* 2014, Beaudrot *et al.* 2016). We divided the park in three sections where potential camera trap locations were established at a density of one sampling site per 2 km^2. We set the camera traps within a 100 m radius of the grid coordinates, in order to select locations with highest probability of recording large mammals. For two camera traps, however, due to extremely dense vegetation, placement was increased from 100 m to a 200m radius from the predetermined grid coordinates.

We surveyed a block of sites for approximately 30 days, and then moved the equipment to survey the next block for approximately the same amount of time. To minimize the probability of changes in occupancy during our study sampling was conducted only in the dry season and in a relatively short period, between 9 July and 13 October 2012. No lure or bait was used to attract animals.

DATA ANALYSIS. —We assembled a detection history matrix for each of the 18 large mammal species recorded, and following previous studies, defined a sampling occasion as seven camera trap days (Gray 2012, Ahumada *et al.* 2013). We analyzed data using the single season occupancy framework, an approach where occupancy and detection parameters are estimated simultaneously using replicated detection/non-detection surveys (MacKenzie *et al.* 2002, Mackenzie *et al*. 2006). In addition to the regular occupancy model (Mackenzie *et al.* 2002), we also obtained occupancy estimates using the Royle-Nichols model, a type of occupancy model where heterogeneity in detection results from variation in the focal organism abundance (Royle & Nichols 2003). We adopted this additional approach as a methodological comparator and to assess reliability.

In our study, it is possible that individuals of some wider ranging species were recorded in more than one camera trap site, failing to meet the assumptions of constant occupancy and of spatial independence among sampling sites (MacKenzie *et al.* 2006). According to MacKenzie *et al.* (2004) this first assumption (constant occupancy) could be relaxed if movement between locations occurred randomly (as it is expected for highly mobile species with large home-ranges), but in this case estimates of occupancy is better interpreted as an estimate of probability of use, and not as probability of occupancy. Hereafter, we interpret our estimates as the probability that a sampling site is used by a given species, an approach adopted in other occupancy studies (*e.g.* Zeller *et al.* 2011, Tobler *et al.* 2015). Not meeting the second assumption (spatial independence among sampling sites) can lead to underestimation of standard errors of occupancy estimates, but this problem can be detected by an assessment of model fit and corrected using a variance inflation factor (Mackenzie *et al.* 2006). Since none of our species models had evidence of lack-of-fit (see the end of this section), we believe this is not a major problem in our study.

We first conducted an exploratory analysis using only the null model (occupancy and detection held constant across sites) to assess each species' detection probability (Mackenzie *et al.* 2002). We defined a cutoff value for detection probability of 0.1, below which occupancy estimates could be biased, leaving ten species to be individually analyzed (Table S1; we also excluded puma due to very imprecise occupancy estimates and lack of convergence in some of the models).

For each of these ten species we fitted further models to investigate the effect of secondary vegetation and of other factors that could potentially affect large mammal occupancy (Table 1). We classified each sampling site according to vegetation succession stage, vegetation physiognomy, shortest distance from potential water sources and shortest distance from the Peruaçu River inside VPSP (Table 1). Within succession stage, secondary habitats were subdivided according to their use in the past: eucalyptus plantation or mixed-use (a mix between charcoal production from native trees and cattle ranching). Camera trap location in relation to trails was treated as a covariate for detection probability (Table 1). Since the number of sampling sites is not particularly large, we fitted univariate models to avoid over parameterization (*i.e.* we did not use models with more than one covariate per parameter estimated).

We tested the community response by combining data from all 18 species in a single matrix, and analyzed it using the single season occupancy framework (Mackenzie *et al*. 2002). Since data from all species were pooled together, occupancy estimates are the probability of use by any of the species in the community, and can be seen as an overall measure of large mammal use. The same process was used as in the species level analysis (seven days grouped as a sampling occasion; occupancy estimates from the regular occupancy and the Royle-Nichols model). Additionally, we added two detection covariates: trophic guild and mass (Table 1). All analyses were conducted using the unmarked package (Fiske & Chandler 2011) for R (R Development Core Team 2015) and all models presented achieved convergence.

We used Akaike Information Criterion (AIC) values to rank and compare models and considered that models with ΔAIC <2 had similar support (Burnham & Anderson 2002). We also assessed goodness-of-fit using the approach developed for occupancy models (Mackenzie & Bailey 2004), implemented in the package AICcmodavg (Mazerolle 2015). We applied the test on the best-supported model according to AIC. Because this test can have lower power in some cases (Mackenzie & Bailey 2004), we defined a significance level of 0.1, below which we considered there was a lack-of-fit for the model. We found evidence of lack-of-fit only for the community level models (P= 0.09; c-hat= 1.23), whereas species-level models appeared to have adequate fit (P> 0.1 for all species). Following Mackenzie & Bailey (2004) we used the quasi-likelihood version of AIC (QAIC) and the square root of the variance inflation factor (c-hat) to adjust SEs of the estimates in the community level models.

Finally, we performed simulations using GenPres (Hines 2006, Bailey *et al.* 2007) to evaluate the effect of different sampling designs on the precision of occupancy estimates (measured by SE) for the four globally threatened species (Table S1). For these simulations we used the values of occupancy and detection probability obtained in the null models.

RESULTS

We recorded 18 large mammal species during this study (Table S1), with a sampling effort of 1898 trap days and an average of 4.6 sampling occasions per sampling site. Results from regular occupancy models (MacKenzie *et al.* 2002) and Royle-Nichols models were very similar for both estimates of occupancy and model ranking (Fig. S1; Table S2). Hereafter we report only the former, as it is frequently used in similar studies (*e.g.* Linkie *et al.* 2007, Ahumada *et al.* 2011, Kinnaird & O'Brien 2012) and also provided more precise estimates (Fig. S1B).

COMMUNITY LEVEL MODELS.—Succession stage was an important factor determining mammal community occupancy (Table 2). Nevertheless, there were similar levels of support for both succession stage and distance from the Peruacu River (waterpa), though QAIC weight of the first covariate was much greater than the second (0.53 and 0.22, respectively – Table 2). Support for the best model where none of the covariates had an effect on occupancy was considerably smaller (ΔQAIC = 2.98; QAIC weight of 0.12 – Table 2).

According to the succession stage model, secondary areas formerly used for eucalyptus plantation had similar community occupancy estimate as old growth areas, counter to our hypothesis (Fig.2A). Secondary/mixed-use areas had a lower occupancy estimate, although the 95% CI overlapped estimates for the other succession stages (Fig 2A). Trophic guild strongly influenced detection probability and was present in all top-ranked models (Table 2); herbivores had the highest and carnivores the lowest detection estimates (Fig. 2B). Models with mass or trail as detection covariate were not supported at the community level (ΔQAIC >60; Table S3).

SPECIES LEVEL MODELS.—Contrary to the community level models, there was little support for the influence of succession stage on individual species' occupancy. Contradicting our predictions, none of the large mammal species that rely on fruits responded negatively to secondary savanna. Occupancy of giant anteater, a species usually favouring open habitats, was not positively affected by secondary habitats. Models with other environmental covariates or with none (null model) had much better support for all species (Table 3). AIC weight for models containing succession stage was lower than 0.05 for seven out of ten species assessed (maximum value for any species was 0.08), and were ranked only as the fifth best-supported model or lower (Table S4).

Though for half of the species assessed (yellow armadillo, striped hog-nosed skunk - *Conepatus semistriatus* -, lowland tapir, white-lipped peccary and Azara's agouti) there is clearly only one covariate influencing occupancy (Table 3), the effect of the environmental factor was not strong, as the estimates overlapped zero.

The effect of camera placement on detection probability was extremely strong for certain species (Table 3). Giant anteater, maned wolf, oncilla (*Leopardus tigrinus*) and lowland tapir were at least five times more likely to be detected if the camera trap was set up on an existing trail. The effect was similar for yellow armadillo and ocelot (*Leopardus pardalis*), though not as strong (*i.e.* estimates overlapped zero).

SAMPLING DESIGN SIMULATIONS.—Both an increase in the total number of sites and the number of sampling occasions (duration of the study) enhanced precision of occupancy estimates for the four globally threatened species recorded (giant anteater, oncilla, lowland tapir and white-lipped peccary). However, the trade-off between sampling occasions and number of sites was non-linear; increasing the number of sampling occasions from five to nine yielded similar gains in precision to increasing the number of sites from 60 to 100 (with five surveys conducted) for all species evaluated (Fig. 3). Standard error below 0.07 was achieved in all survey designs for lowland tapir and in the majority of designs for oncilla and white-lipped peccary, but was not achieved in any design for the giant anteater. Nevertheless, the best improvement in precision (the difference between largest and smallest SE) was found for this last species, whereas for the other three species improvements in precision were modest (Fig. 3).

DISCUSSION

CONSERVATION VALUE OF SECONDARY SAVANNA.—Our study shows that probability of use by any of the individual species investigated is not strongly affected by succession stage, suggesting that secondary savanna areas do not negatively impact large mammals. Most species appeared to have responded to other environmental features, principally physiognomy and distance from water (inside or outside VPSP). While we recognize none of these effects are particularly strong, some of the associations suggested by these well-supported models are in line with other studies, such as preference of denser habitats by agouti (Desbiez *et al.* 2009), and positive relationship with water sources by white-lipped peccary (Keuroghlian *et al.* 2009) and lowland tapir (Padilla & Dowler 1994).

In the community level models, where succession stage may be considered an important factor determining occupancy, the effect is contrary to what we anticipated, with similar estimates for secondary areas that regenerated from eucalyptus and for old growth vegetation. This does not mean all species responded in the same way to secondary habitat; it indicates that probability of use by large mammals in general is not different between secondary savanna areas formerly used for eucalyptus plantation and old growth savanna. Similarities between old growth and secondary habitats have been found in other regions and taxonomic groups, such as amphibians and reptiles in Mexican forests (Hernández-Ordóñez *et al.* 2015), birds in central-African forests (Naidoo 2004) and large mammals in Amazonian forests (Barlow *et al.* 2007). Nevertheless, to our knowledge, this is the first study to explicitly test and observe some similarities in the large mammal fauna of old growth and secondary vegetation in the Cerrado.

There is, however, a suggestion of lower large mammal occupancy in secondary/mixed-use areas. Secondary habitats can be very different even within the same region if they were subjected to different land use or regeneration process (Mesquita *et al.* 2001, Flynn *et al.* 2010). Animals may subsequently respond to those differences, due to variation in resource availability. For example, Bobrowiec & Gribel (2010) found that the type of secondary habitat had a strong effect on bat community composition in the Amazon. Nevertheless, two potentially confounding effects prevent us to make strong inference on the effect of secondary/mixed-use areas. Firstly, sites classified as secondary/mixed-use at VPSP were located further from the park's HQ and with relatively easy access by dirt roads, possibly resulting in higher external pressure, which we were unable to account for in our study. Secondly, secondary/mixed-use areas were further away from the river. Although we used distance from Peruaçu River as a covariate, the fact that secondary/mixed-used areas are clustered together in southern VPSP does not allow us to fully disentangle these two factors. This may also, at least partially, explain the support for distance from the river in the community models.

We make cautious generalizations about large mammal recovery in secondary vegetation within the Cerrado and highlight that our findings cannot be extrapolated to all secondary savannas, especially outside protected lands where the regeneration process tends to be slower and continuous anthropogenic pressure may affect the use of secondary vegetation by wildlife. Our study area might be considered a best-case scenario, as it attained the qualities of a high-value secondary habitat identified by Chazdon *et al.* (2009) and Dent & Wright (2009): proximity of primary habitats, low post-abandonment disturbance and persistence of seed dispersing fauna. Additionally, the relatively short duration of most anthropogenic land-use in the area (around 15 years or less - Gomes & Maillard 2015) favoured the maintenance of a seed bank of native species, synergistically acting with seeds arriving from neighbouring remnants to promote the regeneration after the end of agriculture. As observed by Newbold *et al.* (2015) in a global analysis of land use effects on biodiversity, the conservation importance of secondary habitats depends critically on regeneration time, thus, the advanced state of vegetation regeneration at VPSP is also likely to contribute to its conservation value.

Our results show that Cerrado large mammals, including threatened species, can use secondary habitats that regenerated from clear cut. This finding combined with the large extent to which secondary habitats are represented in our study area and the fact that VPSP currently harbours more than 80% of all large mammals potentially occurring in northern Minas Gerais (Ferreira & Oliveira 2014), indicates that given a favourable habitat history, areas with a large proportion of secondary savanna may still play an important role in maintaining the large mammal community. Although we do not have data on local extinctions and recolonization, we can infer that the occurrence of large mammals in VPSP's secondary areas today may have involved recolonization from nearby vegetation remnants. This might have happened because most secondary areas at VPSP suffered clear cut twice (for the removal of native vegetation to establish eucalyptus plantation and for logging the eucalyptus trees), resulting in large patches of virtually bare land (around 130 km^2 in total) at some point in the past that were unlikely to be used by most large mammal species.

Cerrado large mammals are known to occur in a variety of habitats (Marinho-Filho *et al.* 2002) and may not perceive the environment in a finer scale to respond to the differences in vegetation structure found between old growth and secondary savannas. Thus, while these species can thrive in secondary vegetation, we cannot assume that other animal groups would fare well in secondary savannas. In tropical secondary forests, for instance, recovery is slower for species that are more dependent on habitat structure features (Dent & Wright 2009). A similar pattern could be observed in the Cerrado, as secondary habitats can be structurally different from old-growth ones (Gomes & Maillard 2015). Furthermore, specialized nectarivorous and frugivorous animals might present a strong negative response in secondary savannas, particularly in early regeneration stages, where floristic composition tends to be more different and zoochoric dispersion of fruits is not common (Kuhlmann & Ribeiro 2016).

EFFECT OF TROPHIC GUILD AND TRAIL ON DETECTION PROBABILITY.—Similar to our study, Rovero *et al.*(2014) found that trophic guild is an important factor affecting detection probability for African mammals, with herbivores displaying higher detection than carnivores, an effect likely to be driven by feeding ecology. An alternative explanation is that herbivores tend to occur in higher densities than carnivores (Damuth 1987, Carbone & Gittleman 2002), and as detection probability may be affected by abundance (Royle & Nichols 2003), this could result in herbivores generally having higher detection probability than carnivores.

Although setting a camera trap on a trail had a positive effect on detection for some species, sampling only trails may yield biased results due to an interaction between patterns of animal space-use and the non-random deployment of cameras at locations chosen by researchers (Wearn *et al.* 2013). Similarly, Harmsen *et al.* (2010) showed that, while larger felids are more easily detected on trails, trails may not be well suited for detecting all Neotropical mammal species. In VPSP we recorded three species exclusively off trails. Moreover, focusing sampling on trails may result in unrealistically high occupancy estimates for 'trail-happy' species that cannot be extrapolated to the whole area surveyed, however, the decision on where to set up a camera trap depends largely on objectives of a study.

SAMPLING DESIGN FOR MONITORING.—We have established the baseline against which data from future monitoring initiatives in VPSP could be compared. Similar monitoring implemented in sequential years is being successfully used to evaluate trends in large mammals in protected areas across the world (*e.g.* Ahumada *et al.* 2013, Beaudrot *et al.* 2016). However, the estimation of occupancy in continuous habitats has been criticized, due to the possibility of violating assumptions of constant occupancy and spatial independence (Efford & Dawson 2012). In camera trap studies of large mammals these violations can arise when a species' home-range is very large in relation to the spacing between sampling sites, allowing the same individual to be recorded in more than one site during the survey. Conducting the survey in a relatively short timeframe minimizes these problems, because during the study individuals will only use a small portion of their full home-range. Nevertheless, we adopted the precautionary view of interpreting occupancy as probability of use for all species.

We believe that surveys using 60 camera trap sites, during nine sampling occasions (7-day periods in our study), provides an effective strategy to obtain precise occupancy estimates for some species in the Cerrado. This design yields similar precision to the one surveying 100 sites during five occasions, but with substantially lower costs. However, one must take into account that precision depends on the magnitude of the occupancy estimate, and a SE of 0.07 may be large for a very small occupancy probability. Our decision to conduct more surveys in fewer sites is generally supported by assessments of design trade-offs for occupancy studies (Mackenzie & Royle 2005, Bailey *et al.* 2007), but for rare species maximizing both the number of occasions and sites may be necessary (Mackenzie & Royle 2005, Shannon *et al.* 2014). This is the case for the giant anteater in VPSP, for which a much higher number of sites and/or sampling occasions than the ones used in our simulations was needed to obtain good estimates.

We acknowledge that occupancy and detection probability estimates for a given species is not homogenous throughout its distribution. Although recent studies investigating large mammal occupancy in Brazil have been published (*e.g.* Sollmann *et al.*, 2012; Zimbres *et al.*, 2013), this kind of monitoring remains rare and restricted to few localities. We believe our suggested design may be a useful starting point for new monitoring initiatives, which can then be adapted at new locations as local data becomes available.

ACKNOWLEDGMENTS

Major funding was provided by WWF-Brasil. CNPq, IEF-MG, Panthera, and Idea Wild granted additional funding. Initial data analysis was conducted in a learning exchange funded by the Conservation Leadership Programme. CNPq provides scholarship to GBF and CAPES foundation to IMB and MJRO. We are grateful to João Roberto de Oliveira and his team for helping with logistics, and to IEF-MG for the research permit.

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TABLE 1.*Covariates used to build occupancy models for large mammals at Veredas do Peruaçu State Park*

Covariates	Description	Code	Range of values	Source
Occupancy covariates				
Vegetation succession stage	Succession stage; further divided by type of use in the past	stage	old-growth; secondary/eucalyptus; secondary/mixed-use	Gomes, 2006; information from VPSP manager
Physiognomy	Broad vegetation physiognomy	physiog	cerrado; vereda	Classification in the field
Distance from Peruaçu River[a]	Distance to nearest section of Peruaçu River inside VPSP with water during the dry season peak	waterpa	0.04-16.50 km	Measured on Google Earth Pro
Distance from potential water sources[a]	Distance to nearest location with water during dry season peak	water	0.04-10.10 km	Measured on Google Earth Pro
Detection covariates				
Trail	Location of camera trap in relation to a human trail	trail	on trail; off trail	Classification in the field
Mass[a,b]	Species body mass	mass	1.75-225 kg	Marinho-Filho, Rodrigues & Juarez, 2002
Trophic niche[b]	Species main trophic category	trophic	herbivore; carnivore; omnivore; insectivore; frugivore	Marinho-Filho *et al.*, 2002; Paglia *et al.*, 2012

[a] These covariates were standardized before running the analysis; [b] Used only in the community level models

TABLE 2.*Top ranked models for community level occupancy modelling of large mammals at Veredas do Peruaçu State Park.*

Model	K	QAIC	ΔQAIC	QAICwt
Ψ(stage)p(trophic)	8	1482.145	0	0.5291
Ψ(waterpa)p(trophic)	7	1483.901	1.757	0.2198
Ψ(.)p(trophic)	6	1485.127	2.9828	0.1191
Ψ(water)p(trophic)	7	1485.905	3.76	0.0807
Ψ(physiog)p(trophic)	7	1486.81	4.6658	0.0513

Ψ= occupancy; p= detection probability; K= number of parameters; QAICwt= QAIC weight. Refer to Table 1 for covariates codes. Full set of models presented at Table S3.

TABLE 3.*Top ranked models for species level occupancy modelling of large mammals at Veredas do Peruaçu State Park.*

Species	Ψ	p	K	AIC	ΔAIC	AICwt
Giant anteater						
Ψ(waterpa)p(trail)	+	on trail>off trail*	4	161.27	0	0.72
Ψ(.)p(trail)	NA	on trail>off trail*	3	165.4	4.13	0.09
Yellow armadillo						
Ψ(water)p(trail)	+	on trail>off trail	4	51.79	0	0.60
Ψ(water)p(.)	+	NA	3	54.21	2.42	0.18
Maned wolf						
Ψ(physiog)p(trail)	ver>cer	on trail>off trail*	4	79.13	0	0.27
Ψ(water)p(trail)	-	on trail>off trail*	4	79.42	0.29	0.24
Ψ(waterpa)p(trail)	-	on trail>off trail*	4	79.9	0.77	0.19
Ψ(.)p(trail)	NA	on trail>off trail*	3	79.98	0.85	0.18
Ocelot						
Ψ(.)p(trail)	NA	on trail>off trail	3	61.31	0	0.15
Ψ(.)p(.)	NA		2	61.39	0.086	0.15
Ψ(waterpa)p(trail)	-	on trail>off trail	4	61.61	0.304	0.13
Ψ(water)p(trail)	-	on trail>off trail	4	62.18	0.868	0.10
Oncilla						
Ψ(physiog)p(trail)	cer>ver	on trail>off trail*	4	196.13	0	0.57
Ψ(waterpa)p(trail)	-	on trail>off trail*	4	197.99	1.87	0.22
Ψ(.)p(trail)	NA	on trail>off trail*	3	199.33	3.21	0.11
Hog-nosed skunk						
Ψ(water)p(.)	+	NA	3	99.39	0	0.51
Ψ(water)p(trail)	+	on trail>off trail	4	100.14	0.76	0.35
Tapir						
Ψ(waterpa)p(trail)	-	on trail>off trail*	4	75.73	0	0.77
Ψ(waterpa)p(.)	-	NA	3	79.53	3.8	0.12
Grey-brocket deer						
Ψ(water)p(.)	-		3	232.08	0	0.23
Ψ(.)p(.)	NA	NA	2	232.18	0.1	0.22
Ψ(.)p(trail)	NA	off trail>on trail	3	233.28	1.2	0.13
White-lipped peccary						
Ψ(waterpa)p(.)	-	NA	3	105.75	0	0.62

Ψ(waterpa)p(trail)	-	on trail>off trail	4	107.43	1.68	0.27
Azara's agouti						
Ψ(physiog)p(.)	cer>ver	NA	3	255.53	0	0.50
Ψ(physiog)p(trail)	cer>ver	off trail>on trail	4	255.7	0.17	0.46

Ψ = occupancy; p = detection probability; K = number of parameters; AICw t= AIC weight; cer = cerrado; ver = vereda; + = positive effect; - = negative effect. *Denotes strong effect, where estimate does not overlap zero. Refer to Table 1 for covariates codes. Only top two models or models with AICwt ≥ 0.1 are presented, for full model set see Table S4.

Figures legends

FIGURE 1.Camera trap sites surveyed at Veredas do Peruaçu State Park (VPSP). Triangles are sites in old growth vegetation, crosses are sites in secondary vegetation that regenerated from eucalyptus plantation, circles are sites in secondary vegetation that regenerated from mixed use and the dashed line represents the Peruaçu River. Inset shows Cerrado (dark grey) and PEVP (black) location in Brazil.

FIGURE 2. Estimates and 95% confidence intervals (corrected for overdispersion) for the Ψ(stage)p(trophic) community model. A) Effect of vegetation succession stage over occupancy estimate (Ψ); B) Effect of trophic guild over detection probability (p). Note the differences on the vertical axis.

FIGURE 3. Occupancy estimate standard errors (Ψ SE) for globally threatened species obtained through simulations of sampling designs with different number of camera traps and sampling occasions.

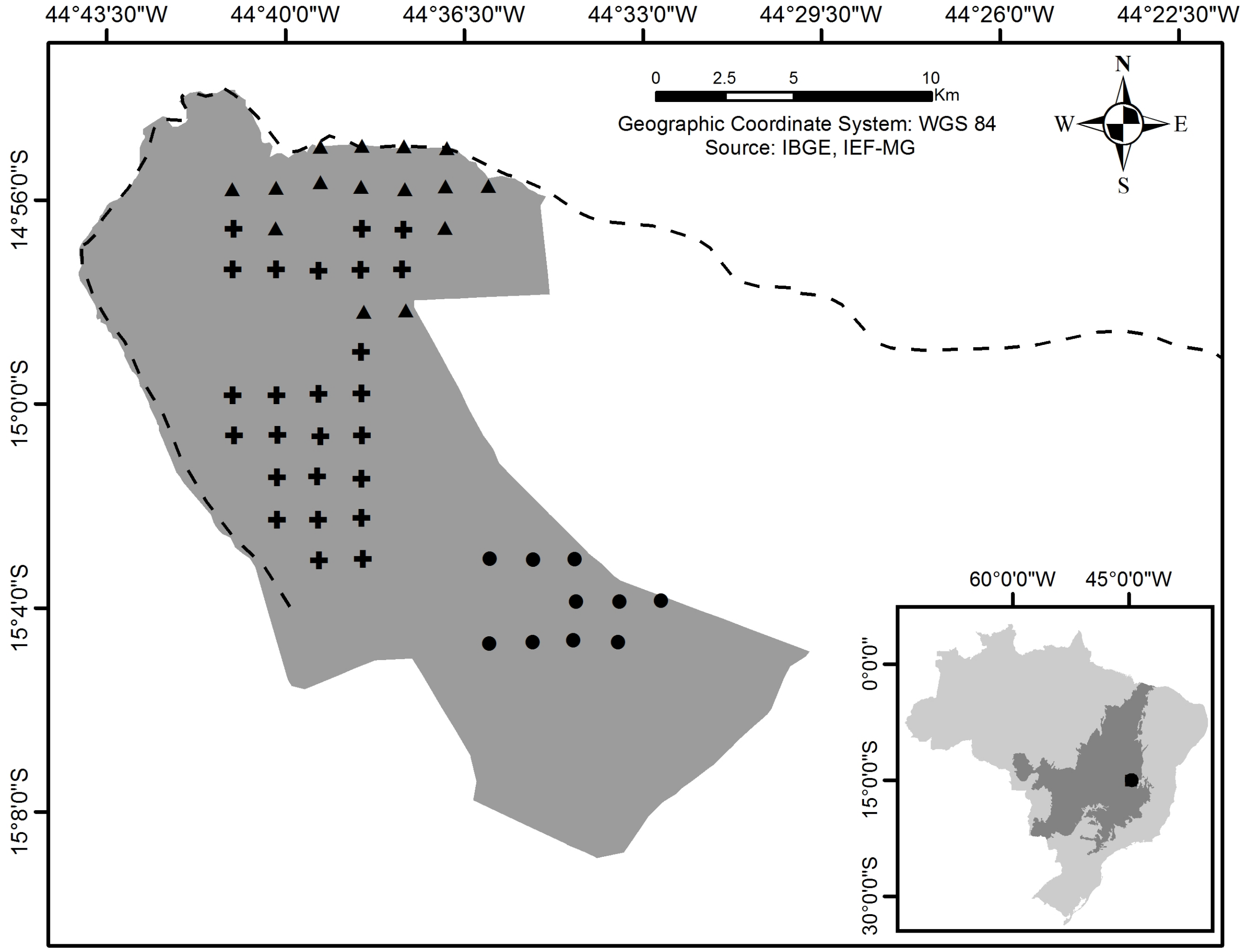

FIGURE 1. Camera trap sites surveyed at Veredas do Peruaçu State Park (VPSP). Triangles are sites in old growth vegetation, crosses are sites in secondary vegetation that regenerated from eucalyptus plantation, circles are sites in secondary vegetation that regenerated from mixed use and the dashed line represents the Peruaçu River. Inset shows Cerrado (dark grey) and PEVP (black) location in Brazil.

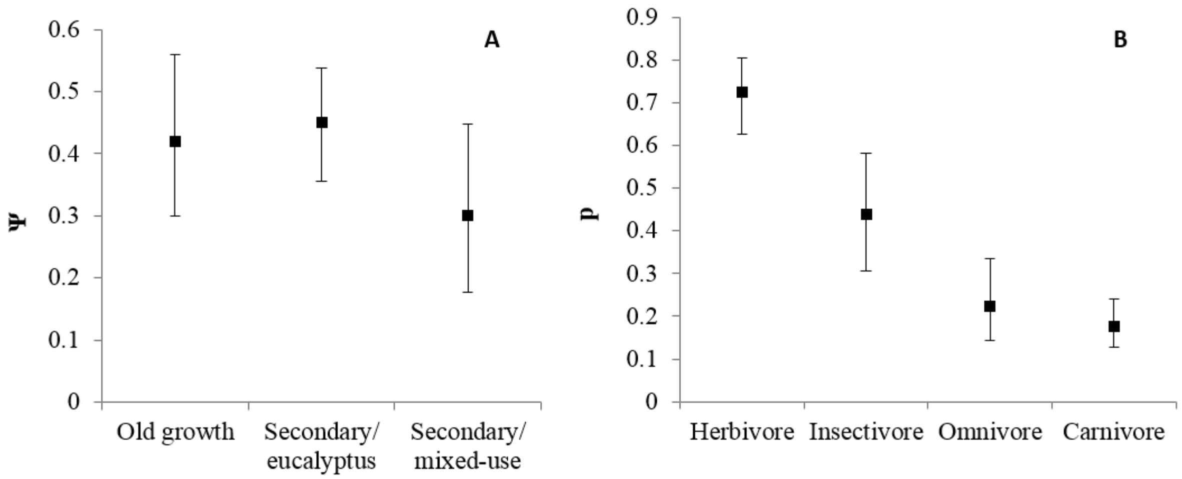

FIGURE 2. Estimates and 95% confidence intervals (corrected for overdispersion)for the Ψ(stage)p(trophic) community model. A) Effect of vegetation succession stage over occupancy estimate (Ψ); B) Effect of trophic guild over detection probability (p). Note the differences on the vertical axis.

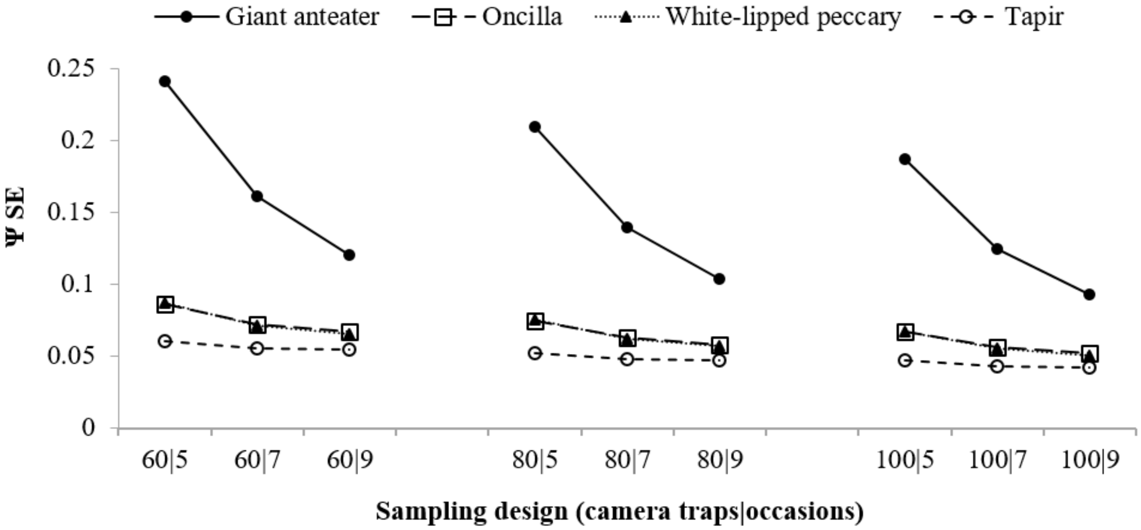

FIGURE 3.Occupancy estimate standard errors (Ψ SE) for globally threatened species obtained through simulations of sampling designs with different number of camera traps and sampling occasions.

SUPPORTING INFORMATION

TABLE S1. *Large mammal species recorded at Veredas do Peruaçu State Park.*

Species	Trophic category	Number of records[a]	Null model detection probability (p)
Pilosa			
Giant anteater(*Myrmecophaga tridactyla*)[b]	in	27	0.139
Cingulata			
Yellow armadillo (*Euphractus sexcinctus*)	in/om	9	0.366
Nine-banded armadillo (*Dasypus novemcinctus*)	in/om	1	0.004
Carnivora			
Ocelot (*Leopardus pardalis*)	ca	7	0.197
Oncilla (*Leopardus tigrinus*)[b]	ca	41	0.290
Puma (*Puma concolor*)	ca	24	0.109
Jaguarundi (*Puma yagouaroundi*)	ca	1	0.004
Crab-eating fox (*Cerdocyon thous*)	om	3	0.013
Maned wolf (*Chrysocyon brachyurus*)	om	10	0.114
Bush dog (*Speothos venaticus*)	ca	1	0.004
Lesser grison (*Galictis cuja*)	om	1	0.004
Tayra (*Eira barbara*)	om	1	0.004
Striped hog-nosed skunk (*Conepatus semistriatus*)	om	15	0.124
Crab-eating raccon (*Procyon cancrivorus*)	om	1	0.004
Perissodactyla			
Lowland tapir(*Tapirus terrestris*)[b]	fr/he	16	0.331
Artiodactyla			
White-lipped peccary (*Tayassu pecari*)[b]	fr/he	17	0.233
Gray brocket deer (*Mazama gouazoubira*)	fr/he	50	0.347
Rodentia			
Azara's agouti (*Dasyprocta azarae*)	fr	65	0.381

[a] Maximum one record per sampling occasion (7 days); [b] Denotes globally threatened species. in=

TABLE S2. *Comparison of model support between regular and Royle-Nichols occupancy models at the community level modelling.*

	K	QAIC	ΔQAIC	QAICwt
Mackenzie model				
Ψ(stage)p(trophic)	8	1482.145	0	0.53
Ψ(waterpa)p(trophic)	7	1483.901	1.757	0.22
Ψ(.)p(trophic)	6	1485.127	2.9828	0.12
Ψ(water)p(trophic)	7	1485.905	3.76	0.08
Ψ(physiog)p(trophic)	7	1486.81	4.6658	0.05
Ψ(stage)p(.)	5	1546.02	63.875	0.00
Ψ(stage)p(trail)	6	1546.264	64.1197	0.00
Ψ(waterpa)p(trail)	5	1547.54	65.3959	0.00
Ψ(stage)p(mass)	6	1547.887	65.7427	0.00
Ψ(.)p(trail)	4	1548.592	66.4475	0.00
Ψ(water)p(trail)	5	1549.445	67.3006	0.00
Ψ(waterpa)p(.)	4	1549.815	67.6707	0.00
Ψ(.)p(.)	3	1550.069	67.9242	0.00
Ψ(physiog)p(trail)	5	1550.474	68.3293	0.00
Ψ(water)p(.)	4	1551.558	69.4134	0.00
Ψ(waterpa)p(mass)	5	1551.624	69.4796	0.00
Ψ(physiog)p(.)	4	1551.841	69.6967	0.00
Ψ(.)p(mass)	4	1551.924	69.7792	0.00
Ψ(water)p(mass)	5	1553.39	71.2455	0.00
Ψ(physiog)p(mass)	5	1553.704	71.5596	0.00
Royle-Nichols model				
Ψ(stage)p(trophic)	8	1475.52	0	0.72
Ψ(waterpa)p(trophic)	7	1478.769	3.2489	0.14
Ψ(.)p(trophic)	6	1480.151	4.6306	0.07
Ψ(water)p(trophic)	7	1481.267	5.7467	0.04
Ψ(physiog)p(trophic)	7	1482.013	6.4927	0.03
Ψ(waterpa)p(trail)	5	1540.526	65.0057	0.00
Ψ(stage)p(trail)	6	1541.597	66.0766	0.00
Ψ(stage)p(.)	5	1542.145	66.6245	0.00
Ψ(water)p(trail)	5	1542.945	67.4252	0.00
Ψ(.)p(trail)	4	1543.177	67.6566	0.00
Ψ(stage)p(mass)	6	1543.884	68.3638	0.00
Ψ(waterpa)p(.)	4	1544.917	69.3968	0.00
Ψ(physiog)p(trail)	5	1545.14	69.6198	0.00
Ψ(.)p(.)	3	1545.885	70.3654	0.00
Ψ(waterpa)p(mass)	5	1546.684	71.1642	0.00
Ψ(water)p(.)	4	1547.034	71.5134	0.00
Ψ(.)p(mass)	4	1547.641	72.1208	0.00
Ψ(physiog)p(.)	4	1547.748	72.2277	0.00
Ψ(water)p(mass)	5	1548.8	73.2801	0.00

Ψ= occupancy; p= detection probability; K= number of parameters; QAICwt= QAIC weight.

Refer to Table 1 for covariates codes.

TABLES3. *Full set of models for the species level occupancy modelling of large mammal at Veredas do Peruaçu State Park*

	K	AIC	ΔAIC	AICwt	cumwt
Giant anteater					
Ψ(waterpa)p(trail)	4	161.27	0.00	0.72	0.72
Ψ(.)p(trail)	3	165.40	4.13	0.09	0.81
Ψ(stage)p(trail)	5	166.56	5.29	0.05	0.86
Ψ(water)p(trail)	4	167.31	6.04	0.04	0.90
Ψ(stage)p(.)	4	167.39	6.12	0.03	0.93
Ψ(physiog)p(trail)	4	167.40	6.13	0.03	0.96
Ψ(waterpa)p(.)	3	169.21	7.94	0.01	0.98
Ψ(water)p(.)	3	169.59	8.33	0.01	0.99
Ψ(.)p(.)	2	169.96	8.69	0.01	1.00
Ψ(physiog)p(.)	3	171.96	10.69	0.00	1.00
Yellow armadillo					
Ψ(water)p(trail)	4	51.79	0.00	0.60	0.60
Ψ(water)p(.)	3	54.21	2.42	0.18	0.78
Ψ(.)p(trail)	3	56.16	4.37	0.07	0.85
Ψ(stage)p(trail)	5	57.10	5.31	0.04	0.89
Ψ(waterpa)p(trail)	4	57.29	5.51	0.04	0.93
Ψ(physiog)p(trail)	4	57.57	5.78	0.03	0.96
Ψ(stage)p(.)	4	58.78	6.99	0.02	0.98
Ψ(.)p(.)	2	60.39	8.60	0.01	0.99
Ψ(waterpa)p(.)	3	60.85	9.07	0.01	1.00
Ψ(physiog)p(.)	3	61.56	9.78	0.00	1.00
Maned wolf					
Ψ(physiog)p(trail)	4	79.13	0.00	0.27	0.27
Ψ(water)p(trail)	4	79.42	0.29	0.24	0.51
Ψ(waterpa)p(trail)	4	79.90	0.77	0.19	0.70
Ψ(.)p(trail)	3	79.98	0.85	0.18	0.87
Ψ(stage)p(trail)	5	82.40	3.27	0.05	0.93
Ψ(physiog)p(.)	3	83.57	4.44	0.03	0.96
Ψ(.)p(.)	2	84.32	5.19	0.02	0.98
Ψ(waterpa)p(.)	3	85.69	6.56	0.01	0.99
Ψ(water)p(.)	3	85.86	6.73	0.01	1.00
Ψ(stage)p(.)	4	87.98	8.85	0.00	1.00
Ocelot					
Ψ(.)p(trail)	3	61.31	0.00	0.15	0.15
Ψ(.)p(.)	2	61.39	0.09	0.15	0.30
Ψ(waterpa)p(trail)	4	61.61	0.30	0.13	0.43
Ψ(water)p(trail)	4	62.18	0.87	0.10	0.53
Ψ(waterpa)p(.)	3	62.39	1.08	0.09	0.62
Ψ(physiog)p(.)	3	62.42	1.11	0.09	0.71
Ψ(physiog)p(trail)	4	62.52	1.21	0.08	0.79
Ψ(stage)p(trail)	5	62.65	1.34	0.08	0.87
Ψ(water)p(.)	3	62.97	1.66	0.07	0.94
Ψ(stage)p(.)	4	63.12	1.81	0.06	1.00
Oncilla					
Ψ(physiog)p(trail)	4	196.13	0.00	0.57	0.57
Ψ(waterpa)p(trail)	4	197.99	1.87	0.22	0.79
Ψ(.)p(trail)	3	199.33	3.21	0.11	0.91

Ψ(stage)p(trail)	5	201.53	5.40	0.04	0.99
Ψ(physiog)p(.)	3	204.82	8.69	0.01	1.00
Ψ(.)p(.)	2	208.58	12.46	0.00	1.00
Ψ(waterpa)p(.)	3	208.83	12.70	0.00	1.00
Ψ(stage)p(.)	4	209.51	13.39	0.00	1.00
Ψ(water)p(.)	3	210.58	14.45	0.00	1.00
Hog-nosed skunk					
Ψ(water)p(.)	3	99.39	0.00	0.51	0.51
Ψ(water)p(trail)	4	100.14	0.76	0.35	0.87
Ψ(waterpa)p(trail)	4	103.89	4.51	0.05	0.92
Ψ(waterpa)p(.)	3	105.13	5.75	0.03	0.95
Ψ(stage)p(.)	4	105.44	6.05	0.02	0.97
Ψ(stage)p(trail)	5	106.25	6.86	0.02	0.99
Ψ(.)p(trail)	3	109.15	9.76	0.00	0.99
Ψ(physiog)p(trail)	4	109.23	9.84	0.00	1.00
Ψ(physiog)p(.)	3	112.65	13.26	0.00	1.00
Ψ(.)p(.)	2	112.98	13.60	0.00	1.00
Tapir					
Ψ(waterpa)p(trail)	4	75.73	0.00	0.77	0.77
Ψ(waterpa)p(.)	3	79.53	3.80	0.12	0.89
Ψ(water)p(trail)	4	80.59	4.85	0.07	0.96
Ψ(water)p(.)	3	81.64	5.91	0.04	1.00
Ψ(stage)p(trail)	5	92.15	16.41	0.00	1.00
Ψ(stage)p(.)	4	92.77	17.03	0.00	1.00
Ψ(.)p(.)	2	101.97	26.24	0.00	1.00
Ψ(physiog)p(.)	3	102.17	26.44	0.00	1.00
Ψ(physiog)p(trail)	4	102.65	26.91	0.00	1.00
Ψ(.)p(trail)	3	102.76	27.03	0.00	1.00
Gray-brocket deer					
Ψ(water)p(.)	3	232.08	0.00	0.23	0.23
Ψ(.)p(.)	2	232.18	0.10	0.22	0.45
Ψ(.)p(trail)	3	233.28	1.20	0.13	0.57
Ψ(water)p(trail)	4	233.77	1.68	0.10	0.67
Ψ(waterpa)p(.)	3	234.05	1.97	0.09	0.75
Ψ(physiog)p(.)	3	234.16	2.07	0.08	0.83
Ψ(waterpa)p(trail)	4	235.25	3.16	0.05	0.88
Ψ(physiog)p(trail)	4	235.28	3.20	0.05	0.93
Ψ(stage)p(.)	4	235.36	3.27	0.04	0.97
Ψ(stage)p(trail)	5	236.29	4.21	0.03	1.00
White-lipped peccary					
Ψ(waterpa)p(.)	3	105.75	0.00	0.62	0.62
Ψ(waterpa)p(trail)	4	107.43	1.68	0.27	0.88
Ψ(water)p(.)	3	110.22	4.47	0.07	0.95
Ψ(water)p(trail)	4	111.64	5.89	0.03	0.98
Ψ(stage)p(.)	4	114.04	8.29	0.01	0.99
Ψ(stage)p(trail)	5	116.03	10.28	0.00	0.99
Ψ(.)p(.)	2	116.20	10.45	0.00	1.00
Ψ(.)p(trail)	3	118.17	12.42	0.00	1.00
Ψ(physiog)p(.)	3	118.19	12.44	0.00	1.00
Ψ(physiog)p(trail)	4	120.16	14.41	0.00	1.00
Azara`s agouti					
Ψ(physiog)p(.)	3	255.53	0.00	0.50	0.50
Ψ(physiog)p(trail)	4	255.70	0.17	0.46	0.96
Ψ(.)p(.)	2	262.98	7.45	0.01	0.97

Ψ(waterpa)p(.)	3	264.75	9.22	0.01	0.98
Ψ(water)p(.)	3	264.97	9.44	0.00	0.99
Ψ(waterpa)p(trail)	4	265.18	9.65	0.00	0.99
Ψ(water)p(trail)	4	265.44	9.91	0.00	1.00
Ψ(stage)p(.)	4	266.16	10.63	0.00	1.00
Ψ(stage)p(trail)	5	266.73	11.20	0.00	1.00
Ψ(stage)p(trail)	5	266.73	11.20	0.00	1.00

Ψ= occupancy; p= detection probability; K= number of parameters; AICwt= AIC weight; cumwt= cumulative AIC weight. Refer to Table 1 for covariates codes.

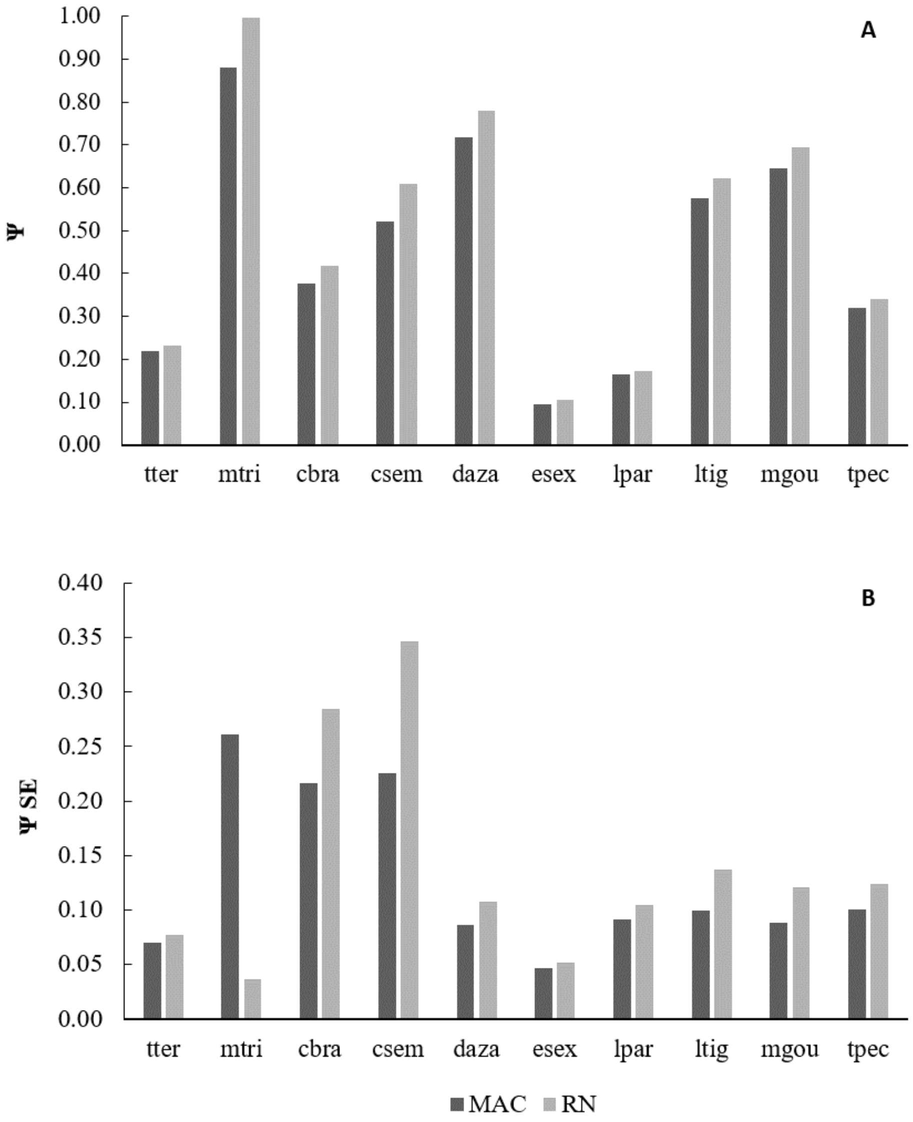

FIGURE S1. Comparison between regular (MAC) and Royle-Nichols (RN) occupancy models at the species level modelling. A) Occupancy estimates (Ψ); B) Standard errors of occupancy estimates (Ψ SE). Species codes composed of first letter of the genus and first three letters of the specific name (refer to Table S1 for species names). Note the differences on the vertical axis.