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ZOOLOGY

Diversity of medium and large neotropical mammals in an area of mixed rain forest

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ABSTRACT. Medium and large mammals (> 1 kg) were studied using camera traps with active sensors in a Conservation Unit located in an area of Mixed Rain Forest or Araucaria Forest (Atlantic Forest at altitude) in the South of Brazil, as a method for investigating the area's conservation status and enabling comparison with other types of environments in which these mammals occur in the Neotropical region. From June 2005 to December 2010, a sampling effort of 10,844 trap-days yielded records of 21 species. A minimum sampling effort of 3000 trap-days was necessary to obtain records of all of these species. The species with the greatest frequency of photocaptures was *Dasyprocta azarae* (agouti), followed by *Leopardus pardalis* (ocelot), *Leopardus guttulus* (southern oncilla or little spotted cat) and *Dasypus novemcinctus* (nine-banded armadillo). The species with the lowest numbers of records were *Pecari tajacu* (collared peccary) and *Chrysocyon brachyurus* (maned wolf). Although the Conservation Unit studied has small physical dimensions, the diversity of species of medium and large mammals was comparable with what has been observed in other types of forests, in particular because there are still effective biological corridors in the area.

Keywords: camera traps; sampling effort; Araucaria Forest; relative frequency; mammalian fauna; Atlantic Rain Forest.

Diversidade de mamíferos neotropicais de médio e grande porte em área de floresta ombrófila mista

RESUMO. Mamíferos de médio e grande porte (> 1 kg) foram estudados com emprego de armadilhas fotográficas com sensores ativos em unidade de conservação em área de floresta ombrófila mista ou floresta com araucárias (Floresta Atlântica de altitude) no sul do Brasil com objetivo de averiguar o status de conservação e permitir a comparação entre diferentes áreas na região Neotropical. No período de junho de 2005 a dezembro de 2010, com esforço amostral de 10.844 armadilhas-dia, 21 espécies foram registradas. O esforço amostral mínimo de 3.000 armadilhas-dia foi necessário para detectar todas estas espécies. A espécie com a maior frequência de foto-capturas foi *Dasyprocta azarae* (cutia), seguida por *Leopardus pardalis* (jaguatirica), *Leopardus guttulus* (gato-do-mato-pequeno-do-sul) e *Dasypus novemcinctus* (tatu-galinha). As espécies com o menor número de registros foram *Pecari tajacu* (cateto) e *Chrysocyon brachyurus* (lobo-guará). Apesar das pequenas dimensões da unidade de conservação estudada, a diversidade de espécies de mamíferos de médio e grande porte foi comparável ao observado em outros tipos de florestas, especialmente devido à presença de corredores ecológicos na região.

Palavras-chave: armadilhas-fotográficas; esforço amostral; floresta com araucárias; freqüência relativa; mastofauna; Mata Atlântica.

Introduction

Mixed Rain Forests, or Araucaria Forests, are primarily distributed in Southern Brazil and are characterized by the Brazilian pine (*Araucaria angustifolia* [Bertol.] Kuntze), a tree species with emergent canopies that spread out above other vegetation (Jarenkow & Budke, 2009). Fossils of members of the Araucariaceae dated from the end of the Triassic period can be found in South America in "petrified forests", especially in Argentina and the South of Brazil (Dutra & Stranz, 2009). Climatic changes over the course of

geological history caused reductions and expansions of the distribution of forests with Araucaria (Bauermann & Behling, 2009). Later, broad-leaved tree species with greater diversity, and generally of tropical origin, formed mixed forests in conjunction with Araucarias, resulting in the Mixed Rain Forest that occurs from the Serra da Mantiqueira (22° S), at an altitude of 1,500 m, as far as Rio Grande do Sul (31° S), in the South of Brazil, at an altitude of 200 m, with higher altitudes compensating for lower latitudes (Backes, 2009).

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Araucaria Forest made up 18% of the Atlantic Rain Forest Biome before European colonization, covering an area of 200,000 km² (Ribeiro & Vieira, 2012), but today it is one of the most fragmented forest types in South America. Araucaria seeds have a very high energy content and production density can be as great as 427 kg ha⁻¹. The highest rates of removal and consumption of araucaria seeds were recorded for small rodents (< 200 g), but these seeds are also an important food resources for medium and large mammals (Iob & Vieira, 2008).

The area of distribution of the Araucaria Forest is similar to the areas of the Pantanal and Campos Sulinos (pampas) biomas, but the species richness of mammals is greater in Araucaria Forest (Ribeiro & Vieira, 2012). There are no records of species of mammals that exclusively occur in this type of forest, probably because eurybiomic species (those with the capacity to adapt to different types of biomas) developed in South America in response to contraction and expansion of different types of biomas because of climatic changes (Bofarull, Royo, Fernández, Ortiz-Jaureguizar, & Morales, 2008). Studies of the mammals living in this type of environment (Cademartori, Fabián, & Menegheti, 2004), (Cademartori, Marques, & Pacheco, 2008), (Iob & Vieira, 2008), (Vieira & Iob, 2009) tend to demonstrate the behavioral adaptations of these animals to this forest type, which has Araucaria as its iconic tree species, the seeds of which have been a food source for successive assemblages of animals over the geological history of South America.

Camera traps have made it easier to study medium and large mammals in forests (Rowcliffe & Carbone, 2008). However, to avoid distorted interpretations of results, there is a need to understand many different aspects of the lives of these animals, such as species-specific behavior, body size, size of living area, or stochastic variations (Tobler, Carrillo-Percastegui, Pitman, Mares, & Powell, 2008). Medium and large mammals have been studied living in several different types of vegetation in the Neotropical region including Tropical Forest in Central America (Harmsen, Foster, Silver, Ostro, & Doncaster, 2009), in the Andes (Lucherini et al., 2009), in Montane Cloud Forest (Jiménez et al., 2010), in Amazonian pre-Andean Seasonal Forest (Gómez, Wallace, Ayala, & Tejada, 2005), in transitional areas between the Cerrado and Amazonian Forest with secondary forest that are subject to flooding in the rainy season (Negrões, Revilla, Fonseca, Soares, Jácomo, & Silveira, 2011), in an area with Cerrado savanna vegetation (Trolle, Bissaro, & Prado, 2007), in Cerradão (woodland savanna) in a patchwork

comprising Eucalyptus silviculture and sugar cane plantations (Lyra-Jorge, Ciochetti, Pivello, & Meirelles, 2008), in Atlantic Rain Forest in medium to advanced stage of regeneration in patchworks of pasture, agriculture, and exotic silviculture (Espartosa, Pinotti, & Pardini, 2011), in Dense Rain Forest and Coastal Forest (Oliveira-Santos, Tortato, & Graipel, 2008), and in Semi-deciduous Seasonal Forest in a subtropical climate (Kasper, Mazim, Soares, Oliveira, & Fabián, 2007).

The objectives of this article are to analyze the diversity of medium and large mammals (> 1 kg) in a long-term study conducted in Mixed Rain Forest or Araucaria Forest (Atlantic Rain Forest in a subtropical climate) comparing the results with those of studies undertaken in other types of forest and to determine the sampling effort that must be employed with camera traps to detect the majority of terrestrial species.

Material and methods

Study area

The study was conducted in the São Francisco de Paula National Forest (FLONASFP), located in Rio Grande do Sul, Brazil's Southernmost state, at geographical coordinates (29°23'45.6"S 50°22'54.0"W). This is a Conservation Unit with a sustainable use classification, it has an area of 1,606.7 ha (16 km²), and it is located in the Araucaria High Plains at a mean altitude of 930 m. The vegetation comprises a mosaic of natural vegetation made up of Mixed Rain Forest (901.9 ha) and plantations of native pine (Araucaria angustifolia) and silviculture of exotic Pinus sp and Eucalyptus sp species. The region's climate is humid subtropical (Cfb on the general Köppen-Geiger system). Mean annual precipitation is 2,240 mm with no dry season and temperatures recorded for the coldest month (winter) vary from -6.5 to 28°C and for the hottest month (summer) from 4.5 to 34°C (Cademartori, Marques, Pacheco, Baptista, & Garcia, 2002).

The assemblage of mammals recorded in the region includes at least 66 species of native wildlife and one exotic species, 30 of which are medium to large (Marques, Cademartori, & Pacheco, 2011).

Sampling in the field

Camera traps (10 analog camera traps set in pairs on either side of a track) with active sensors (Marques & Ramos, 2001) were used to record the presence of medium and large mammals, with body mass greater than 1 kg (Chiarello, 2000). The camera traps were placed along unpaved tracks that cross the forest, providing routes for animals and, sporadically, people

and conservation unit service vehicles, and also along tracks through the forest only used by animals. The sites where camera traps were set were not chosen specifically because they offered greater numbers of places animals could shelter. No bait was used, infrared transmitters and receptors were set at 10 to 18 cm from the ground, depending on the degree of irregularity of the ground, and the distance between sampling stations was 500 m. The sampling effort expended was 10,844 trap-days from June/2005 to December/2010, continuously. Equipment was switched on 24 hours a day and sampling was conducted throughout all months of the year. Only one photocapture per species in any given 1 hour interval was considered in analyses, in order to maintain sampling independence.

Definition of frequency of occurrence in samples

Species were classified by frequency of detection on the basis of the following relative frequencies of records: Constant (> 10%); intermediate (10 to 1%), or sporadic (< 1%).

Definition of species' diets

The basis for classification of the mammals' diets is from Paglia et al. (2012). *Dasypus novemcinctus* was considered an insectivore and grouped with *Cabassous tatouay* and *Tamandua tetradactyla*. Scientific names for mammal species are as Wilson and Reeder (2005).

Statistical analyses

The potential number of species in the area was estimated using first and second order Jackknife,

Chao 1, ACE, and Bootstrap estimators, calculated using EstimateS 8.1 software (Colwell, 2001). BioEstat 5.3 was used to conduct Kruskal-Wallis analysis of variance of capture success by year (Ayres, Ayres, Ayres, & Santos, 2007).

Results

A total of 21 species of medium and large mammals were recorded by photocapture from June 2005 to December 2010 (Table I).

A total of 2026 independent photocaptures were a success rate of 0.187 recorded with photocaptures/trap-day or 18.7 photocaptures for every 100 trap-days. The mean number of photocaptures per day was 0.99, varying from 0.93 in 2005 to 1.09 in 2009. with no significant variations different vears (H=2.5655)p=0.7666). The species with the greatest frequency of photocaptures was Dasyprocta azarae, followed by Leopardus pardalis, Dasypus novemcinctus, and Leopardus guttulus. Species with intermediate photocapture frequencies were Procyon cancrivorus, Mazama gouazoubira, Didelphis aurita, N. nasua, Eira barbara, Puma concolor, Leopardus wiedii, Puma yagouaroundi, and Cerdocyon thous. Species with low frequencies of photocaptures were Tamandua tetradactyla, Lycalopex gymnocercus, Galictis cuja, Cuniculus paca, Cabassous tatouay, Didelphis albiventris, Pecari tajacu, and Chrysocyon brachyurus (Table I). A sampling effort of around 3000 trap-days was needed to obtain photographic records of all 21 species (Figure 1).

Table 1. Independent photocaptures of medium and large mammals recorded in the São Francisco de Paula National Forest (Brazil) from June, 2005 to December, 2010.

Species	N. Ind. Cap.	Diet	Regularity in sampling
Didelphis albiventris Lund, 1840 – white-eared opossum	1	Fr/On	Sporadic
Didelphis aurita (Wied-Neuwied, 1826) – big-eared opossum	176	Fr/On	Intermediate
Dasypus novemcinctus Linnaeus, 1758 – nine-banded armadillo	206	In/On	Constant
Cabassous tatouay (Desmarest, 1804) – greater naked-tailed armadillo	2	Myr	Sporadic
Tamandua tetradactyla (Linnaeus, 1758) – lesser anteater	13	Myr	Sporadic
Dasyprocta azarae Lichtenstein, 1823 - agouti	409	Fr/Gr	Constant
Cuniculus paca (Linnaeus, 1766) - paca	7	Fr/Hb	Sporadic
Pecari tajacu (Linnaeus, 1758) - collared peccary	1	Fr/Hb	Sporadic
Mazama gouazoubira (G. Fischer, 1814) – gray brocket deer	178	Fr/Hb	Intermediate
Galictis cuja (Molina, 1782) - lesser grison	7	Ca	Sporadic
Eira barbara (Linnaeus, 1758) - tayra	77	Fr/On	Intermediate
Nasua nasua (Linnaeus, 1766) - coati	103	Fr/On	Intermediate
Procyon cancrivorus (G. Cuvier, 1798) – crab-eating raccoon	196	Fr/On	Intermediate
Lycalopex gymnocercus (G. Fischer, 1814) – pampas fox	8	Ca/On	Sporadic
Cerdocyon thous (Linnaeus, 1766) - crab-eating fox	32	In/On	Intermediate
Chrysocyon brachyurus (Illiger, 1815) – maned wolf	1	Ca/On	Sporadic
Leopardus wiedii (Schinz, 1821) – margay	46	Ca	Intermediate
Leopardus guttulus (Hensel, 1872) – southern little spotted cat	205	Ca	Constant
Leopardus pardalis (Linnaeus, 1758) – ocelot	266	Ca	Constant
Puma concolor (Linnaeus, 1771) – puma, cougar or mountain lion	55	Ca	Intermediate
Puma yagouaroundi (E. Geoffroy Saint-Hilaire, 1803) – jaguarondi	37	Ca	Intermediate

No. Ind. Cap.: Number of independent captures; Ca: carnivore; Fr. frugivore; Gr. granivore; Hb: herbivore; In: insectivore; Myr: myrmecophage; On: omnivore (diets as per Paglia et al., 2012); L. guttulus (= L. tigrinus from South and Southeast Brazil) according to Trigo et al. (2013).

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The species with the largest number of photocaptures, *Dasyprocta azarae* (Table I), is a frugivore-granivore. Analysis of the proportions of photocaptures of species in different dietary categories revealed the following frequencies: 30.41% carnivores (six species), 29.37% herbivores (including frugivores and granivores) (four species), 29.31% omnivores (eight species) and 10.91% insectivorous (three species).

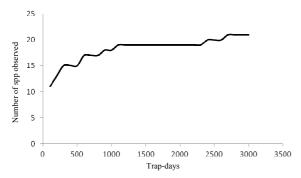


Figure 1. Accumulation curve for species of medium and large mammals photocaptured in the FLONASFP from June, 2005 to December, 2010.

The species richness estimators indicated the potential occurrence of at least 26 species of medium and large mammals in the area studied. The lowest estimates (22 species) were produced using the Bootstrap and Chao 1, the ACE and first-order Jackknife estimated 24 species, and the highest estimate was produced using the second-order Jackknife estimator (Figure 2).

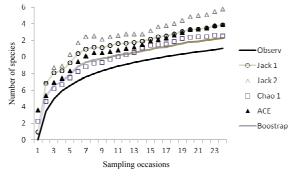


Figure 2. Curves illustrating results for estimates of richness of species of medium and large mammals photocaptured in the FLONASFP from June, 2005 to December, 2010.

The majority of species were present in all of the years sampled, with high, medium, or low frequencies of photocaptures. However, there were species with low frequencies of photocaptures, some of which only occurred in 1, 2, 3, 4 or 5 years, and one species (*Didelphis aurita*) with a high frequency of photocaptures that first appeared in 2007 and was only captured in 4 different years (2007 through 2010).

Discussion

Photocaptures or their rates of records are an estimate of relative frequency of use or of activity (Espartosa et al., 2011) in the environments sampled and do not necessarily reflect the abundance of these species. Capture frequencies are a poor indicator of relative abundance because sampling is impacted by factors such as: species-specific behavior (road use or not, partially arboreal or exclusively terrestrial, specialist or generalist in given types of habitat), body size, size of living area (animals with larger living areas move around more and, theoretically, would have greater opportunity to pass through a site with a camera trap) or stochastic variations (major differences in the capture of different species between two sampling campaigns) (Tobler et al., 2008). If fieldwork protocols are applied in a similar manner in different places, the rates of photocapture can be used to compare assemblages of mammals between different environments (Espartosa et al., 2011) or over time in a single location.

Using active sensors with infrared transmitters and receivers aligned at a low height from the ground allows smaller animals to be detected, including small rodents and marsupials and small birds such as doves and passerines. Therefore, the low number of records of smaller species such as Galictis cuja is unlikely to be an artifact of the method employed. Smaller animals have not been effectively recorded using camera traps with passive sensors (Tobler et al., 2008); (Lyra-Jorge et al., 2008) that detect temperature differences caused by the presence of animals with body temperature different from the ambient temperature. Comparisons of the effectiveness of camera traps and sand track plots for detection of medium and large mammals that have been conducted in other studies led to the conclusion that, over the long term, using camera traps can economize resources because researchers do not need to remain in the field throughout the sampling campaign (Lyra-Jorge et al., 2008). Over the short term, sand track plots enabled detection of slightly more species than camera traps, but identification of some species of the genera Mazama and Leopardus (Espartosa et al., 2011) and Mazama and Dasypus (Lyra-Jorge et al., 2008) was only possible using photographic trapping. In the study described here, only one small deer of the genus Mazama that was recorded photographically, was not identified to the species level, because without DNA analysis it is impossible to be sure of their identification (personal communication from Dr. José Maurício Barbanti Duarte).

The proportions of feeding strategy categories detected among the medium and large mammals in the FLONASFP can be considered well distributed. Studies undertaken with camera traps in seven areas of tropical forest in Africa, Asia, and South and Central America indicate that there are higher numbers of omnivorous and herbivorous species, followed by carnivores and insectivores, and that the dominant species are herbivores (Ahumada et al., 2011). This pattern was also observed in Mixed Rain Forest, where there were eight omnivorous species (Didelphis albiventris, D. aurita, Eira barbara, N. nasua, Procyon cancrivorus, Lycalopex gymnocercus, Cerdocyon thous, Chrysocyon brachyurus), four herbivorous (Dasyprocta azarae, Cuniculus paca, Pecari tajacu, Mazama gouazoubira), six carnivores (Galictis cuja, Leopardus wiedii, L. guttulus, L. pardalis, Puma concolor, P. yagouaroundi), and three insectivores (Tamandua tetradactyla, Cabassous tatouay, Dasypus novemcinctus) and Dasyprocta azarae (frugivore-granivore) was the dominant species. Although Paglia et al. (2012) classify both Dasypus novemcinctus and Cerdocyon thous as insectivores/omnivores, the proportion of insects and other invertebrates in the diet is considerably greater for the first of these species (McBee & Baker, 1982) than for the canid, which is extremely opportunistic and has a much more diverse diet (Parera, 2002).

The photocapture success rate of 0.187 photos/trap-day, with records of 21 species, was not dissimilar to 0.208 photos/trap-day with records of 19 species achieved in Mexico (Monroy-Vilchis, Zarco-González, Rodríguez-Soto, Soria-Díaz, & Urios, 2011). In short-term studies in primary Amazonian forest in Peru, success rates were 0.353 photos/trap-day photos/trap-day, and 0.348 recording 21 and 27 species respectively (Tobler et al., 2008). In a study with a duration of 2 years conducted in the Parque Estadual do Turvo, Rio Grande do Sul, Brazil, in a semi-deciduous seasonal forest environment with subtropical climate, using a sampling effort of 2,154 trap-days, 25 species were recorded with success rates of 1.32 and 1.03 records /trap-day on two roads cutting through the forest (Kasper et al., 2007). In terms of capture success, Mixed Rain Forest in a region with fragmented natural environments had a smaller relative frequency of medium and large mammals. The studies mentioned in this comparison did not employ bait and did not set camera traps close to animals'shelters, just along unpaved roads and tracks through the vegetation (Kasper et al., 2007; Monroy-Vilchis et al., 2011) as in this study, or forming a grid with sampling points spaced at 1km or 2km intervals (Tobler et al., 2008). In principal,

using bait to attract animals to camera traps or installing the equipment close to potential shelter does increase the likelihood of obtaining records of the animals studied. However, it is not a viable method for studies conducted with the objective of obtaining quantitative data on abundance and density, since it can change animals' behavior. Capture success rates can reflect two phenomena: the density of animals that occur in an area or the frequency with which they use these areas. Forests with dense vegetation at ground level can make it difficult for land animals to move around, causing them to seek natural or manmade trails. Positioning camera traps along such trails may increase capture success rates. The short-term effectiveness of camera traps may be questionable for detection of species (Carvalho, Rosalino, & Esbérard, 2016), because not all species that occur in a given area will be photo-captured quickly. The capture success rate of 0.187 photos/trap-day could be considered ineffective for a short period, but over many years of study it was sufficient to enable identification of 21 of the 30 species of medium and large mammals that occur in the Araucaria High Plains (Marques, Cademartori, & Pacheco, 2011). The major advantage of employing camera traps is the possibility of comparing study areas over the long term, as has been done for subtropical Atlantic Forest in Santa Catarina (Bogoni, Giehl, Oliveira-Santos, & Graipel, 2016).

The second-order Jackknife species richness estimator predicts that at least 26 species of medium and large mammals are likely to be present in the area studied. Species of this size that occur in the region but which were not recorded by the camera traps during the study period include Lontra longicaudis (long-tailed otter), Myocastor coypus (coypu), Hydrochoerus hydrochaeris (capibara), Alouatta guariba (brown howler monkey), Conepatus chinga (Molina's hog-nosed skunk), Ozotocerus bezoarticus (pampas deer) and Mazama sp (small deer) (Marques et al., 2011). The first three of these species are semi-aquatic, the howler monkey is arboreal, and the hog-nosed skunk and pampas deer live in open environments, so there is therefore a very low probability of obtaining photographic records very low to the ground in forest environments. Terrestial mammals are more likely to be detected than arboreal and semi-aquatic species (O'Brien, Kinnaird & Wibisono, 2011). Although Lontra longicaudis and Alouatta guariba are present in the Parque Estadual do Turvo, camera traps also failed to detect them in that park (Kasper et al., 2007).

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Richness estimates are needed when the observed data do not attain an asymptote (Gotelli & Colwell, 2001). A sampling effort of at least 1000 trap-days is recommended for estimating species richness (O'Brien et al., 2011). After a sampling effort of 2000 trap-days, the asymptote of the sampling sufficiency curve for the medium and large mammals studied in the FLONASFP appeared to have been attained with 19 species recorded. However, after 3000 trap-days, 21 species had been recorded, with the addition of Pecari tajacu and Chrysocyon brachyurus (Marques & Fabián, 2013), and the estimator curves no longer appeared to have attained an asymptote. The greater the number of rare species, the higher the probability that there will be species present that have not been sampled (Gotelli & Colwell, 2001). Jackknife estimators are the most appropriate for cumulative species data (O'Brien, 2008) because they are less dependent on hypotheses of species richness distribution and are based on the sampling process rather than curve fitting, while, along the same lines, the Chao estimator relaxes the assumption of equal capturability or detectability for each species across sampling efforts (O'Brien et al., 2011).

The study that is most appropriate for comparison with the results of the present study was conducted in the Parque Estadual do Turvo (PET) (27°00'S 53°40'W to 27°20'S 54°10'W) and used camera traps to study medium and large mammals in Semi-deciduous Seasonal Forest (Kasper et al., 2007). In theory, this type of environment can support the same species of mammalian fauna that occur in the Araucaria High Plains region. Species that only occurred in the PET were Panthera onca (jaguar), Tapirus terrestris (tapir), Sylvilagus brasiliensis (Brazilian cottontail) and Cebus nigritus (= Sapajus nigritus) (black capuchin), while the species Cabassous tatouay, Lycalopex gymnocercus, Chrysocyon brachyurus. and Mazama gouazoubira were only recorded in the FLONASFP. Among the group only found in the FLONASFP, the first three occur in open environments that form mosaics with Mixed Rain Forest in the Araucaria High Plains, whereas the PET is in a region with a patchwork completely dominated by agriculture and so is less likely to support grassland species. The species that were only recorded in the PET are, basically, forest species and depend on this type of environment in a well conserved state for their survival. Although Panthera onca can also live in open environments, it has become extinct in the Araucaria High Plains where livestock farming caused persecution of this predator. Other notable differences between the two areas were Leopardus tigrinus (= L. guttulus), which is

considered rare in the PET, but was constant in the FLONASFP, and *Pecari tajacu*, which is common in the PET, but only recorded sporadically in the FLONASFP. This last was only recorded along a narrow trail that descends a hillside in the direction of a water course and, probably, has suffered intensive pressure from hunting in the Araucaria High Plains, becoming rare and inconspicuous.

Conclusion

The area of the FLONASFP is around 10% of the size of the PET, but there is intensive agriculture around the PET Conservation Unit and the Uruguay river runs along the border with Argentina, where there are forest remnants. Although the FLONASFP is much smaller, it is located in a region in which the predominant economic activities are still livestock farming and silviculture and there are biological corridors in the form of native forests and areas that have difficult access, such as canyons, where medium to large fauna is able to survive. Medium to large mammalian fauna has survived in this region where Araucaria Forests still exist.

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