

Universidade Federal de Minas Gerais
Instituto de Ciências Biológicas
Programa de Pós-Graduação em Ecologia
Conservação e Manejo da Vida Silvestre

Abundância, densidade, padrões de atividade e ecologia espacial de felinos silvestres no Parque Estadual do Rio Doce - MG

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Belo Horizonte
Setembro 2019
Universidade Federal de Minas Gerais

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Abundância, densidade, padrões de atividade e ecologia
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- MG

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ATA DE DEFESA



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Ata da Defesa de Tese

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Ricardo Corassa Arrais

No dia 27 de setembro de 2019, às 14:00 horas, na sala 162, bloco B2 do Instituto de Ciências Biológicas da Universidade Federal de Minas Gerais, teve lugar a defesa de tese de doutorado no Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre, de autoria do(a) doutorando(a) Ricardo Corassa Arrais, intitulada: "**Abundância, densidade, padrões de atividade e ecologia espacial de carnívoros no Parque Estadual do Rio Doce - MG**". Abrindo a sessão, o(a) orientador(a) e Presidente da Comissão, Doutor(a) Fernando Cesar Cascellli de Azevedo, após dar a conhecer aos presentes o teor das normas regulamentares do trabalho final, passou a palavra para o(a) candidato(a) para apresentação de seu trabalho. Estiveram presentes a Banca Examinadora composta pelos Doutores: Sandra M. C. Cavalcanti (INSTITUTO PRÓ-CARNÍVOROS), Rogério Cunha de Paula (CENAP), Diego Guimarães Florencio Pujoni (UFMG), Luciano Martins Verdade (USP) e demais convidados. Seguiu-se a arguição pelos examinadores, com a respectiva defesa do(a) candidato(a). Após a arguição, apenas os senhores examinadores permaneceram no recinto para avaliação e deliberação acerca do resultado final, sendo a decisão da banca pela:

- Aprovação da tese, com eventuais correções mínimas e entrega de versão final pelo orientador diretamente à Secretaria do Programa, no prazo máximo de 30 dias;
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- Reformulação da tese com indicação de nova defesa em data estabelecida a critério do Colegiado em observância às Normas Gerais da Pós-graduação na UFMG e ao Regimento do PPG-ECMVS;
- Reprovação

A banca indica esta tese aos Prêmios CAPES e UFMG de teses? SIM NÃO

Nada mais havendo a tratar, o Presidente da Comissão encerrou a reunião e lavrou a presente ata, que será assinada por todos os membros participantes da Comissão Examinadora.

Belo Horizonte, 27 de setembro de 2019.

Comissão Examinadora	Assinatura
Doutor(a) Fernando Cesar Cascellli de Azevedo	
Doutor(a) Sandra M. C. Cavalcanti	
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Doutor(a) Luciano Martins Verdade	

DEDICATÓRIA



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EPIGRAFE

Tudo parece ousado para aquele que nada se atreve”
Fernando Pessoa



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RESUMO

Durante o período de 2015 a 2019, estudei aspectos básicos da ecologia de felinos silvestres no Parque Estadual do Rio Doce – PERD, no estado de Minas Gerais, Brasil. Utilizando câmeras-traps e modelos espaciais e não espaciais de captura-recaptura, comparei estimativas de abundância e densidade de jaguatiricas (*Leopardus pardalis*) entre estações do ano e utilizando estratégias diferentes de instalação das câmeras (aleatória e sistemática). O sucesso de captura (média de 2.5 registros/100 armadilhas/noite) e as densidades obtidas com o design sistemático foram altos comparados a outros estudos, especialmente utilizando modelos não espaciais. Obtive também maior sucesso de captura na estação seca do que na chuvosa (3.2 registros/100 armadilhas/noite na estação seca e 1.8 registros/100 armadilhas/noite na estação chuvosa). Em geral, a instalação sistemática de câmeras produziu estimativas mais precisas e menores intervalos de confiança. Ainda utilizando câmeras-traps, descrevi os padrões de atividade de carnívoros em geral e calculei a sobreposição temporal entre jaguatiricas, onças-pintadas (*Panthera onca*) e onças-pardas (*Puma concolor*) e suas presas potenciais. Obtive 11.078 registros de 34 espécies de vertebrados. Neste estudo, fêmeas de onças-pintadas, pardas e jaguatiricas foram consideradas dilassificadas como catemerais, enquanto machos de onças-pardas e jaguatiricas foram classificados como predominantemente noturnos. Encontrei uma alta sobreposição temporal entre estas três espécies de felinos e com suas presas potenciais. Apresento também os primeiros resultados referentes à ecologia espacial de onças-pintadas e onças-pardas monitoradas simultaneamente na Mata Atlântica. Utilizando colares-GPS, monitorei duas onças-pintadas e cinco onças-pardas, durante 405 dias em média, totalizando 17.929 localizações. Estimei então o tamanho das áreas de vida de onças pintadas (195.66 km² em média) e de onças pardas (216.262 km² em média). Ambas as espécies apresentaram territórios menores que em outros estudos na Mata Atlântica. Observei também uma alta sobreposição entre áreas de vida dos indivíduos monitorados, variando entre 17 e 89%. Ambas as espécies selecionaram habitats naturais ao invés de áreas antrópicas. Este estudo forneceu informações novas e modernas sobre a ecologia de carnívoros na Mata Atlântica, preenchendo uma lacuna importante de conhecimento, podendo contribuir para a conservação e o manejo a longo prazo destas espécies na Mata Atlântica.

ABSTRACT

From 2015 to 2019, I studied basic aspects of carnivore ecology in the Rio Doce State Park - RDSP, Minas Gerais state, Brazil. Using cameras-trap and spatial/non-spatial capture-recapture models, I compared estimates of ocelot (*Leopardus pardalis*) abundance and density using different camera deployment strategies (random and systematic) and between seasons (dry and wet). The capture success (2.5 records/100 trap-nights in average) and density estimates obtained with the systematic design were high compared to other studies, especially for non-spatial models. I obtained higher capture-success in the dry season than in the wet season (3.2 records/100 trap-nights, 1.8 records/trap-nights, respectively). In general, the systematic installation of cameras produced more accurate estimates and smaller confidence intervals. Still using camera-traps, I described the activity patterns of carnivores and quantified the temporal overlap between ocelots, jaguars (*Panthera onca*) and pumas (*Puma concolor*) and their potential prey. I obtained 11,078 records from 34 vertebrate species. In this study, female jaguars, pumas and ocelots were classified as cathemeral, showing more significant activity during the day, while male jaguars and ocelots were mainly nocturnal. I found a high temporal overlap between these three felid species and their potential prey. I also present the first results concerning the spatial ecology of jaguars and pumas monitored simultaneously in the Atlantic Forest. Using GPS-collars, I tracked two jaguars and five puma for 405 days on average, totaling 17,929 locations. Then I estimated the size of home ranges of jaguars (195.66 km² in average) and pumas (216.262 km² in average). Both species showed smaller territories than in other studies in the Atlantic Forest. I observed a high overlap between monitored individuals, ranging from 17 to 89%. Both species selected natural habitats instead of anthropic areas. This study provided new and modern information on the ecology of carnivores in the Atlantic Forest, filling an important knowledge gap and may contribute to the conservation and long-term management of these species in the Atlantic Forest.

INTRODUÇÃO GERAL

Mamíferos carnívoros representam um papel significativo na estrutura e funcionalidade dos ecossistemas (Steneck, 2005; Ritchie & Johnson, 2009; Wirsing *et al.*, 2017), influenciando na composição das comunidades de presas e de outros predadores (de Oliveira & Pereira, 2014; Pérez-Irinea & Santos-Moreno, 2016). Apesar de sua importância, a maioria dos carnívoros neotropicais, especialmente os felinos, sofreram grande declínio populacional devido à perda de habitat e à caça, levando ao seu desaparecimento em grandes porções de sua distribuição original (Salom-Pérez *et al.*, 2007), como na Mata Atlântica (Beisiegel, Sana & Moraes, 2012; Paviolo *et al.*, 2016). Embora originalmente cobrindo 139.584.893 hectares (ha), atualmente resta apenas 16.377.472 ha (11,73%) da cobertura original de Mata Atlântica. A maior parte é distribuída principalmente em pequenos fragmentos (<100 ha) isolados uns dos outros (Silva *et al.*, 2007; Ribeiro *et al.*, 2009).

Em Minas Gerais, o Parque Estadual do Rio Doce (PERD) desempenha um importante papel na proteção da biodiversidade, pois é um dos maiores fragmentos de Mata Atlântica do estado, onde os três maiores felinos neotropicais (Emmons & Feer, 1997; Oliveira, 2002; IUCN, 2016): onças-pintadas (*Panthera onca*), onças-pardas (*Puma concolor*) e jaguatiricas (*Leopardus pardalis*) ainda ocorrem simpatricamente (Viana, 2006; Keesen, Valle Nunes & Scoss, 2016). Diversos estudos descreveram estas espécies separadamente, mas poucos investigaram as interações ecológicas entre eles ao mesmo tempo e no mesmo lugar (Scognamillo *et al.*, 2003; Gonzalez-Borrajo, López-Bao & Palomares, 2017).

Para que haja coexistência, carnívoros simpátricos tem que compartilhar recursos, interagindo no espaço e no tempo (Schoener, 1974; Gordon, 2000). Para entender como esta assembleia de felinos neotropicais coexiste, procurei nesta tese,

responder questões importantes à respeito da ecologia básica destes felinos no PERD, utilizando um conjunto de dados obtidos através do Projeto Carnívoros do rio Doce, que desde 2015 vem coletando dados acerca dos carnívoros na região através de armadilhas fotográficas, captura e monitoramento de onças usando coleiras-GPS (Global Positioning System).

No primeiro capítulo, utilizando registros de câmeras-trap, utilizei duas abordagens para estimar a abundância e densidade de jaguatiricas no PERD na estação seca e na estação chuvosa e comparei os resultados com o objetivo de avaliar as diferenças entre as abordagens e estações do ano. Já no segundo capítulo, também utilizando registros de câmeras-trap, para compreender como carnívoros interagem entre si e com suas presas na escala temporal, descrevi os padrões de atividade de onças-pintadas, onças-pardas e jaguatiricas, quantifiquei a sobreposição entre elas e também com suas potenciais presas. Finalmente, no último capítulo abordei a escala espacial, para compreender como estas espécies utilizam o seu habitat, estimei então o tamanho das áreas de vida, sobreposição entre territórios, e verifiquei houve seleção por algum determinado tipo de ambiente em algum período do dia.

Palavras-chave

Câmeras-trap, Captura-recaptura, *Coexistência*, Área de vida, *Leopardus pardalis*, *Panthera onca*, *Puma concolor*, *Partição temporal*, Ecologia espacial.

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CAPÍTULO I – Manuscrito para submissão – PLOS ONE
Camera-trap placement strategy for robust estimation of Ocelot (*Leopardus pardalis*) abundance and density in the Atlantic Forest

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Abstract

Monitoring variation in population features such as abundance and density is fundamental in the evaluation and implementation of conservation actions, and camera-traps have become an important tool in studies aiming to assess population occupancy or trend. Camera deployment may follow a variety of strategies ranging from random to systematic placement, and robust sampling design is needed to obtain unbiased estimates. We compared estimates of ocelot (*Leopardus pardalis*) abundance and density from random and systematic camera deployment designs by using capture-recapture measures with consideration for spatial dynamics. We found that ocelot estimates varied according to the chosen sampling design and modeling approach, with recapture success and density estimates being higher with non-random design especially for non-spatial models. In terms of seasonality, we detected higher capture success in dry season for non-spatial models. In general, systematic camera deployment yielded more precise population estimates owing to lower within-sample variance. Although our study strongly supports the general principle of strategic placement of cameras for robust population estimation, we urge caution when applying population estimation models beyond the original study region where model parameters were first developed.

Key words: Camera trapping, *Leopardus pardalis*, Deployment, Sampling design, Random, Systematic, Non-random, Spatial models, Non-spatial models

Introduction

A fundamental concept in population status assessment is the need to obtain reliable estimates of abundance and density [1]. Abundance is a population feature of especially central interest because it affects virtually every aspect of species biology [2,3] and reliable estimates are necessary for the development of effective conservation strategies [4]. However, estimating population density of solitary and elusive forest carnivores can be challenging [5,6], and to obtain reliable estimates of carnivore population size and density, a robust and efficient sampling methodology is required [7]. Camera-trap studies are increasingly used to document species presence/absence, estimate population abundance and density, and assess species richness and community structure [8]. Although contemporary cameras have a number of features that improve their ability to detect a variety of animal species, broad-scale installation of cameras can be cost-prohibitive and impractical, leading researchers to deploy a limited set of cameras in a smaller space. It follows that such deployments should be designed in a manner that achieves robust sampling design and sampling efficacy [9,10], but in general these concerns are rarely tested. A number of sampling designs are available for camera deployment in the wild, ranging from completely random to fully systematic [11]. A random approach [e.g., [12,13]] allows the researcher to sample a wider area and range of habitats while also facilitating simultaneous estimation of abundance for unmarked animals, as many recent studies assessing density estimates for unmarked animals rely on this approach [14]. Broad sampling is especially important in carnivore research because it also may provide the necessary spatial context for assessment of prey diversity and abundance, or to extend inference to other regions or study systems. However, some authors recommend a systematic sampling design for cryptic species, including

many wild carnivores, whereby camera-traps are positioned on trails and roads or in baited sites, thereby augmenting both the sample of occurrence records as well as recapture events [13–18]. This approach could be advantageous by increasing sampling efficiency and decreasing costs [7,14,19,20], but it does also have risks, including potentially biased sampling [7].

Camera trapping is increasingly used to generate density estimates through capture-recapture models. When generating density estimates, it is necessary to know the sampling area from which animals are sampled (i.e., effective trapping area - ETA) which is obtained by estimating mean maximum distance of movement (MMDM) of individuals, which can be considered as a proxy for home-range diameter [21]. Indeed, some studies indicate that a one MMDM buffer is superior for estimating ETA and corresponding density of cryptic species [22], which may be especially relevant for elusive terrestrial carnivores. The size of the area from which animals are sampled is normally estimated ad hoc [14], implying that the precise delineation of the ETA may vary depending on the approach used. It follows that this may affect the reliability of resulting density estimates [23]. Moreover, traditional capture-recapture models do not take into consideration the specific location of camera traps despite that probability of an individual's capture depends on the overlap between its home range and the trap deployment scheme [24]. Accordingly, animals with home ranges that are partially outside the range of camera traps may compromise the reliability of density estimates because they induce heterogeneity in encounter probabilities [25]. More recently, spatially-explicit capture-recapture (SECR) models have sought to address the above concerns by using detection location of individuals to calculate activity centers, distance parameters, and encounter rates at the activity center to refine detection probabilities and occupancy estimates. Indeed, the SECR approach

considers the probability that an animal will be captured as a function of the distance between camera-trap locations and its estimated activity center [24,26]. Notably, SECR models are less sensitive to the spatial setup of camera stations compared to nonspatial models [27], thereby allowing for standardized trapping arrays to serve in estimating population density, potentially across multiple study areas [23]. Because the SECR approach avoids selection of an arbitrary buffer distance when estimating the ETA [26,28–30], it may provide a superior density estimate compared to those derived from alternative models. Notwithstanding these potential advantages, to date studies have not clearly tested the performance of spatially-explicit versus non-explicit capture-mark-recapture models for estimating density of terrestrial carnivores, and how sampling design can affect the accuracy and precision of estimates.

The ocelot (*Leopardus pardalis*) is a solitary mid-sized felid found in the Americas having mainly nocturnal and crepuscular habits [31–35]. Ocelots feed mainly on small mammals and are habitat generalists, having variable home range sizes depending on several factors like habitat structure, prey availability, geographical location and gender [35–37]. Although ocelots are widely distributed and classified as "least concern" [38], their distribution has constricted during recent decades owing mainly to habitat loss and persecution associated with livestock depredation [39,40]. In Brazil, ocelots are relatively widespread, with the Atlantic Forest serving as a core region of occurrence [38,41]. It follows that testing sampling designs for effective ocelot population estimation is well-suited for such a region, with the expectation that refined methods can then be applied to regions where ocelots are of high conservation concern. Ocelots can be individually identified by their body marks, making it possible to use capture-recapture methods to assess abundance and population density [39,42–44]. We used random and systematic camera traps

deployment to determine ocelot abundance and density estimates, and predicted that: 1) estimates would vary accordingly to the approach used in camera deployment; 2) capture success would be higher using systematic approach, owing to the biased sampling of animals in locations providing higher detectability (i.e., roads and trails) [42]; 3) capture success would be higher during the dry season since animals tend to move higher distances in order to find resources [45]; 4) density estimates from spatial-explicit models be more precise than non-explicit models, yielding relatively smaller standard errors because those models consider animal movements and allow incorporating site-specifics and individual covariates [13].

Materials and methods

Ethics statement

We used camera-traps to detect ocelots in the study area. This technique does not interfere with animal behavior, as there is no direct contact. The research project was authorized by the local authority under the research permits: ICMBio/SISBIO: 93896765/2015-2016 and 54311277/2016-2017.

Study area

The Rio Doce State Park - RDSP is a conservation unit in the state of Minas Gerais, southeastern Brazil (19°29' - 19°48' S / 42°28' - 42°38' W). The park covers approximately 360 km², representing one of the largest continuous remnants of Atlantic Forest in Brazil and the largest in the state of Minas Gerais [46]. In addition to ocelots, the RDSP includes a variety of carnivores such as pumas (*Puma concolor*), margay cats (*Leopardus wiedii*) and jaguars (*Panthera onca*) [38]. The

RDSP represents an important area for maintenance of biodiversity in the Atlantic Forest [47], and vegetation is classified as submontane seasonal semideciduous forest [48,49]. The climate is classified as humid subtropical, with two marked seasons: a rainy summer from October to March followed by a dry winter from April to September [50].

Sampling design

We used random and systematic placement positioning of capture stations to estimate ocelot abundance and density. We used camera traps (Bushnell© Trophy Cam Natureview, Trophy Cam Standard and Trophy Cam Essential - Kansas, USA) and 16GB memory cards (SanDisk© - California, USA) to establish capture stations (hereafter 'stations'). Stations included a pair of camera-traps installed at 40-50 cm in height that were fixed to trees and facing each other: this design allowed us to typically record both flanks of a given animal, thereby facilitating individual identification by spots, marks and scars [14]. Cameras were programmed to record 10-30 second HD videos, with an interval of 60 seconds between videos. All cameras were programmed to operate simultaneously for 24 hours/day, over a period of 40 days per wet and dry season, totaling 80 days of camera data. We did not use baits or any kind of attraction.

In the random placement design, we positioned stations at pre-defined buffers that covered the entire RDSP area. Due to lack of roads and access in remote areas of the RDSP, we opened 340 km of trails to access designated stations. To improve station access we divided the area into two sectors: north and south, each including 9 circular zones (buffers) that were 5.0 km in diameter. This size represents twice the size of the smallest conservatively-estimated home range size for female jaguars

(initial target-species; 10 km² in a Central America tropical forest habitat) [51]. In each buffer, we used a random number generator to define 3 random locations, indicating where the trap cameras should be installed (Figure 1A), resulting in 27 stations per sector and a total of 54 stations in both sectors. We used a minimum distance of 1.5 km between stations, which represents a sampling intensity that should be sufficient to potentially detect all individuals in the population [14,20,52,53]. Every time a selected point fell less than 1.5 km from another one inside a buffer, it was discarded and another point was randomly generated, leading to a suitably spaced camera distribution and implying that our 'random' sampling design was restricted to ensure adequate spatial coverage. In each season (dry and rainy) the survey lasted a maximum of 120 days, which represents a short period in relation to the longevity of ocelot lifespan and migratory movements of individuals. The entire survey (rainy plus dry) occurred over 11 months, with stations being installed for 40 days in the northern RDSP sector, followed by removal and installation in the southern sector for each season. It is likely that few/any ocelots were available for detection in both areas, and the setup/takedown periods lasted ~ 20 days, allowing the period for active data collection from cameras to span the dry (April 30 - August 25, 2016) and rainy (November 25, 2016 - March 3, 2017) seasons. We did not consider camera trap data during the period when not all cameras were functional at the same time.

Map of study area at Rio Doce State Park

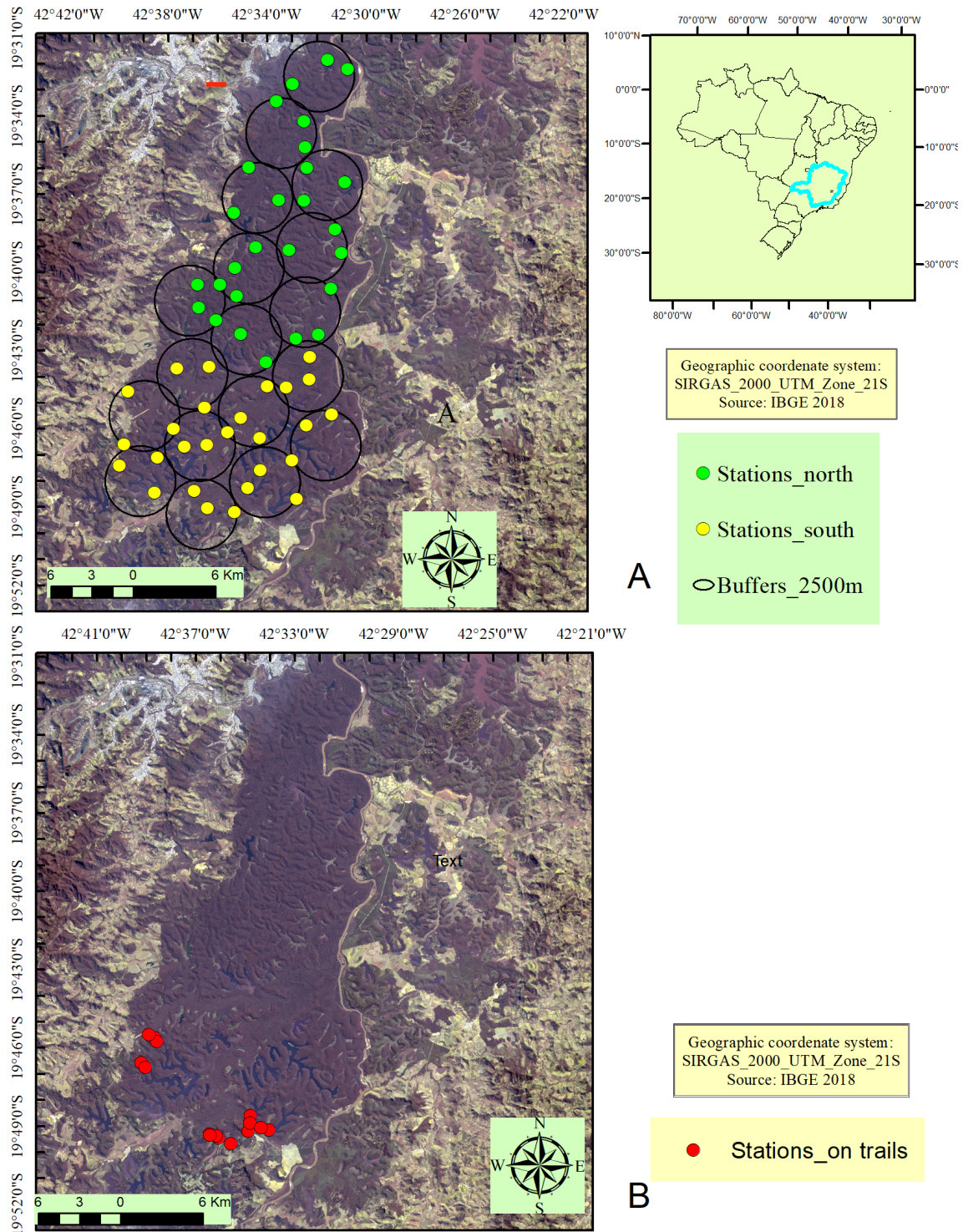


Fig 1. Distribution of buffers and stations in Rio Doce State Park during the ocelot camera trapping study. Black circles indicate 2.5km buffers. Green and yellow circles represent stations installed during random placement in North and South sectors respectively (A). Red circles represent stations installed during systematic placement (B). Insets show the position of Minas Gerais State in Brazil and the position of Rio Doce State Park.

For our systematic sampling design, 15 stations were installed in the southern RDSP sector (Fig. 1B) along low-traffic (<1 vehicle / day) unpaved roads which are used rarely and exclusively for research and maintenance. The location of stations was assigned to maximize capture probability of ocelots by systematically selecting sites having direct evidence (e.g., tracks, scraps, scats) indicating ocelot presence. Instead of standardizing distance between stations (as per the random sampling design described above) in this case station distance ranged from 0.3 - 10 km. Note that for this design ocelot home range size was not considered and only a small portion of the southern sector was sampled relative to the random sampling design. We considered that our non-random approach more realistically reflected cost restrictions and logistical challenges that are characteristic of many carnivore camera-trapping studies of carnivores [54]. Accordingly, our smaller sample size and biased selection of camera deployment sites was strategically designed to increase ocelot detection probability. For our non-random design the sampling period spanned dry (July 8 to August 16, 2017) and rainy (October 2 to November 10, 2017) seasons.

Ocelot identification

We identified ocelots by analyzing collected video footage when to observe the unique color and marking patterns of individuals. Ocelots are relatively easy to distinguish because of their mostly unique rosette and stripe patterns [42]. We considered as a single record all captures of the same individual at a given station that were collected over a 24-hour period. Not all individuals had the right and left flanks registered in the same record, and when only one flank was registered but the individual had already been identified in another trapping event, this record was

maintained. When it was not possible to accurately identify the animal, this record was discarded although these records served to calculate capture-success. In total, obtained 244 ocelot detections, of which 159 (65.2%) allowed the identification of 47 different individuals (29.6 % of all identified records). Ocelot sex was determined by the presence or absence of testes [42].

Data analysis

We used the Density © Software (Wellington, New Zealand) [55] to obtain ocelot abundance and population density estimates, first using closed capture-recapture models (CR) based on individual recognition. Analyses were conducted using both buffers (1/2 MMDM and 1 MMDM) to allow for broader comparison to other studies [6,20,43,56]. We considered the effective trapping area (ETA) as the total area covered by these buffers. For spatial models, we selected maximum likelihood spatially-explicit capture-recapture (ML-SECR) closed population model because this approach addresses primary limitations of capture-recapture techniques [57]. For estimating model parameters we used the Jackknife estimator, which is robust [58,59] and better captures heterogeneous behavior expected for different individuals and studies with small sample sizes [58].

After identifying individual ocelots, we developed encounter histories for each individual for inclusion in capture-recapture models. Detection probability was improved by considering 5 consecutive days of survey as a single occasion [58,59]. In order to calculate capture success, we divided total number of ocelot records (including records in which it was not possible to identify individual ocelots) by the total number of trap-nights. We checked the assumption of population closure within each season using the software MARK, as described by Trole and Kery, 2003 [42].

Results

For the random placement design, we obtained 107 capture records, of which 64.5% were in the dry season. We identified individual ocelots in 50 records, with 60.0% being in the dry season. Dry season capture success was 3.2 records/100 trap-nights compared to 1.8 records/100 trap-nights in the wet season (average 2.5 records/100 trap-nights). After excluding repeated captures of the same individual within a 24-hour period, we tallied with 31 individual ocelots of which 8 were females, 13 were males and 10 were of unknown sex. Population closure tests confirmed that the population was closed during each season (Table 1). When analyzing both seasons together, the best model indicated an effect of season on recruitment (births and migrations) of ocelots, indicating a lack of population closure (Table 1). Our sampling effort for the random placement totaled 4,320 trap-nights, and during the dry season 21 different individuals yielded an estimated population size of 54.5 ± 12.7 individuals using non-spatial models. During the rainy season 16 individuals (only 3 recaptures) led to an estimated 54.9 ± 13.1 individuals. When combined, the open-population estimate was 114.0 ± 20.9 individuals (Table 2).

For the systematic placement approach, we obtained 137 records, with 98 (71.5%) in the dry season and 39 (28.5%) in the rainy season. We identified ocelots at the individual level in 104 records, with 83 (79.8%) in the dry season and 21 (20.2%) in the rainy season. Capture success was 16.3 records/100 trap-night in the dry versus 6.5 records/100 trap-night in the wet season, for a combined rate of 11.4 records/100 trap-nights. The 12 ocelots detected in the non-random design included 6 females, 4 males and 2 indeterminate individuals. Importantly, we found that all estimated population sizes for the systematic approach based on non-spatial models yielded smaller estimates than from the random approach, which was expected given

the smaller portion of the study area sampled. The estimated population size during for the dry season was 10.7 +/- 1.9 individuals in an area of 36 - 75 km² (1/2 and 1 MMDM, respectively) (Table 2). In the rainy season, we recorded 8 different individuals, generating an estimated population of 9.0 +/- 1.6 individuals. When combining the stations, for which we had 4 individuals in common, we obtained an estimated population of 13.2 +/- 2.9 individuals (Table 2).

Density estimates for the random approach using non-spatial models were in general 46 to 69% smaller than those using the systematic approach (Table 2). For instance, for the dry season density estimates were 13.78 and 15.29 individuals/100 km² (1MMDM and 1/2 MMDM, respectively) for the random approach, while for the systematic approach they were approximately two times higher (19.87 and 28.15 individuals/100 km² (1MMDM and 1/2 MMDM, respectively) (Table 2). For the rainy season, the 13 different ocelots had too low probability of detection to yield a robust population density estimate. Density estimates for the random approach using spatial models were comparable than those from the systematic approach, with density estimated for the dry season being 14.04 individuals/100 km² and 12.60 individuals/100 km², respectively (Table 3) and, for the rainy season 35.92 and 24.60 individuals/100 km², respectively

Discussion

Recently developed spatial explicit capture-recapture methods have advanced our knowledge in using space encounter information on individuals in order to model density and other spatial aspects of animal population structure. Nonetheless these potential advantages, to date studies have not clearly tested the performance of spatially-explicit and non-explicit capture-mark-recapture models for estimating density of terrestrial carnivores. Moreover, the effectiveness of combining sampling and the analytical approach for reliably estimating density of elusive species such as the ocelot have yet to be tested. In our study, we obtained different density estimates according to the approach used (i.e. random or systematic placement of camera-traps). For instance, using non-spatial models for the systematic approach, the estimated density for the dry season was two times higher than in the random-approach (Table 2). When evaluating the seasons combined, the estimated density was up to 8.2 times higher than that obtained through the random-approach. When comparing non-spatial to spatial models, density estimates with non-spatial models were up to 2 times higher than those obtained using spatial models in the random-approach, and up to 11 times higher in the systematic-approach. Although for both spatial and non-spatial models, density estimates obtained using the random-approach were smaller than density estimates obtained in the systematic-approach, we should be cautious in interpreting our results, particularly for spatial models that are more robust to variation in sampling design. For instance, for the dry season, density estimates obtained for the systematic-approach were 1.4 – 1.9 times higher than those obtained for the random-approach (Table 3). When we analyzed the seasons combined, density estimates were up to 1.3 times higher for the systematic-approach than for the random-approach.

However, we observed very large overlapping confidence intervals between approaches. Therefore, our results for spatial models don't support the hypothesis that density estimates would vary according to the sampling approach used. RDSP is a heterogeneous protected area and a much smaller and homogeneous area was covered during data collection in the non-random compared to the random approach. The area sampled in the systematic approach has many water sources throughout the year and is the only sampled area with unpaved roads with restricted traffic, thus the difference in ocelot abundance and density between approaches, particularly for non-spatial models, might be a reflection of this heterogeneity, ETA size and the differences in sampling designs used. The preference of some felines to use roads or animal trails instead of crossing the dense forest has been already reported [60,61], and old unpaved roads with restricted traffic can either serve as traditional routes or territorial boundaries, a behavior also observed in jaguars in Belize [51]. Specifically for ocelots, a higher rate of captures on dirt roads than on open trails in the forest has already been recorded [39]. Therefore, it is possible that the greater number of recaptures on roads reflected this behavior. Another behavior that may explain the greater detection on roads is the hunting strategy, because felines such as ocelots may prefer to move on cleaner ground, avoiding noise when stepping on dry leaves and branches and announcing their presence to potential prey [62].

In our study, using the random-approach, it was possible to estimate density for the dry season and for seasons combined (dry and rainy) simultaneously, but no estimation was possible for the rainy season alone due to the low probability of detection. Estimates based on capture probabilities less than 0.1 are considered to be inaccurate [42], especially for small populations ($n \leq 50$) where reliability is further reduced if there is a high level of heterogeneity in the probability of capture within the

population, even when using the Mh Jackknife estimator [63]. However, in the systematic placement approach, we found \hat{p} values greater than 0.1, indicating greater robustness and confidence in the estimates obtained in dry and rainy seasons. Regarding seasonality, we observed higher densities in the rainy season than in the dry season, as reported in other studies [21,64]. This difference may be related to reduced movement in the rainy season, when animals tend to concentrate in areas where there are permanent water sources and dense vegetation [45]. It is also worth noting that we had very similar density estimates between the two approaches (random and systematic) in the dry season using spatial models. The observed differences in detection and density at different seasons indicate that long-term monitoring should be seasonal and consistent over time. The low recapture success in such a short period (90 days) between seasons, considering the longevity of the species, may be an indicator of temporary emigrations and/or different habitat use related to water availability and this should be taken into consideration in the planning of further studies.

The capture success obtained in the systematic placement approach was similar to that obtained in other studies with ocelots in different biomes [39]. As we expected, capture success in the systematic-approach was on average 4.5 times higher than in the random-approach, especially in the dry season where we obtained the highest reported capture success. Despite a 3.6 times larger sample effort in the random approach, the total number of ocelot records was 21.9% lower compared to the total systematic placement-approach. In both approaches we obtained more records in the dry season than in the rainy season (Table 2). Population closure tests indicated that the population was closed in both dry and rainy seasons separately but not when analyzing the seasons together (Table 1), mostly due to the lack of

recapture events. Therefore, caution is recommended when interpreting results of both seasons together.

We obtained differences in sex determination in our study probably due to the difficulty in observing the testes area of adult ocelots and very young individuals depending on their position while being recorded by the cameras. The difficulty in determining sex has already been reported in other studies with ocelots, which determined sex for approximately 75% of adult individuals [55]. With the cameras positioned on unpaved roads, animals tend to be recorded following the road direction, passing perpendicular to the cameras, which facilitates the observation of the presence or absence of testes. The greater number of individuals of unidentified sex in the random-approach may be related to the greater difficulty in visualizing the testes area of adult individuals when ocelots are recorded in different positions in relation to the camera trap. In addition, in other carnivore species, females have lower capture rates because they move less, have smaller territories and use habitat differently than males. Females of other carnivore species tend to avoid camera-traps more than males [65]. In this context, our results regarding sex ratios should be interpreted cautiously, particularly for the random-approach, where more records were discarded because of the difficulty in identifying the sex of some individuals.

Density estimates vary throughout ocelot's distribution [22,42,66], probably due to heterogeneity of habitats (prey density, for example) and characteristics of the sample design (number of camera traps, distance between sampling points, sampling effort, effective trapping area, and random and non-random camera-trap positioning) [67]. Our most optimistic estimate obtained in this study for the entire RDSP (114 +/- 20.9 animals) considering the possibility of individual migration between seasons, suggests an alarming situation for the conservation of ocelots,

given the isolation of the RDSP and the persistence of threats to the species in the region. Processes of fragmentation and loss of habitat in the surrounding landscape have been intensified over recent years, for instance, with the construction of a road that passes along the park and is currently being paved (increasing the risk of roadkills), and the presence of domestic dogs and poachers frequently recorded within the RDSP. These results reinforce the importance of the RDSP for the conservation of the species in the region, since the population viability of ocelots depends on the maintenance and protection of large preserved areas. For ocelots and other endangered species, RDSP may represent their last refuge. However, the conservation of the RDSP and all species within its boundaries will only be possible if this Conservation Unit is monitored and protected, threats in the surroundings are mitigated, and ecological corridors are established and maintained to increase connectivity to other protected areas.

Regarding the approaches and models herein used, we found that the differences in the standard errors of abundance estimates indicate that the systematic placement approach resulted in more precise estimations than random placement. It is a consensus that the positioning of camera traps on unpaved roads increases the probability of detection of cryptic species. However, the data obtained in this study indicate that caution should be taken in extrapolating these data to heterogeneous and larger areas than the ones that were sampled. This restricted area, where unpaved roads are located, represents approximately 5% of RDSP total area (based on MMDM estimators). Therefore, the extrapolation of abundance estimates to heterogeneous or larger areas can lead to mismanagement decisions and can compromise the viability of populations, especially small populations in fragmented areas.

Conclusion and recommendations

In our study, we found that seasonality is an important factor for comparisons between these estimates, nevertheless further studies are necessary to investigate this relation. Several studies do not even cite the season of the year in which the survey was conducted. We emphasize the importance of disseminating this information, since the estimates varied between the dry and rainy seasons in the same area as reported in our study. Differences in the success of detecting individuals between dry and rainy seasons indicate that long-term monitoring should be seasonally consistent over time. Otherwise, differences in ocelot numbers due to seasonal differences may be misinterpreted along the years. The increasing number of studies using camera-traps and capture-recapture models to estimate density, particularly for felines, makes the standardization of techniques essential for comparative analysis, both between different sites and the monitoring of the same area over the years [41]. The present study provides information to assist future research in the choice of more appropriate methods that may generate more accurate estimates and be replicated, especially for cryptic or endangered species occurring at low densities. We recommend continuity in the monitoring of this population and surveys of adjacent areas to determine the occurrence of ocelots, as well as studies of ocelot spatial ecology and habitat selection with special attention to seasonality. This information is fundamental to determine the viability of this population, and to identify areas necessary to maintain the connectivity among populations of ocelots in the region.

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Table 1. Population closure test results accordingly to season

Season	Model	AICc	Delta AiCc	AICc Weight	Model Likelihood	No. Par.	Deviance	-2Log(L)
Dry	{phi(1)p(.)f(0)}_phi_f_fixed	75.4195	0	0.76002	1	1	6.3782	73.229
	{phi(.)p(.)f(.)}	78.0642	2.6447	0.20255	0.2665	3	3.9502	70.801
	{phi(t)p(.)f(0)}_f_fixed	82.637	7.2175	0.02059	0.0271	4	5.564	72.4148
	{phi(1)p(.)f(t)}_phi_fixed	83.187	7.7675	0.01564	0.0206	4	6.114	72.9648
	{phi(t)p(.)f(t)}	88.3175	12.898	0.0012	0.0016	7	0	66.8508
Rainy	{phi(1)p(.)f(0)}_phi_f_fixed	46.6471	0	0.92667	1	1	0.5053	44.3614
	{phi(.)p(.)f(.)}	52.3114	5.6643	0.05457	0.0589	3	0.4553	44.3114
	{phi(t)p(.)f(0)}_f_fixed	55.6805	9.0334	0.01012	0.0109	4	0.1882	44.0442
	{phi(1)p(.)f(t)}_phi_fixed	55.9978	9.3507	0.00864	0.0093	4	0.5053	44.3614
	{phi(t)p(.)f(t)}	71.8561	25.209	0	0	7	0	43.8561
Dry + Rainy	{phi(dry_rainy)p(.)f(dry_rainy)}	165.2227	0	0.99985	1	5	153.4045	153.4045
	{phi(1)p(.)f(0)}_phi_f_fixed	183.1044	17.8817	0.00013	0.0001	1	180.9963	180.9963
	{phi(.)p(.)f(.)}	187.1427	21.92	0.00002	0	3	180.457	180.457
	{phi(t)p(.)f(t)}	227.7655	62.5428	0	0	15	176.8986	176.8986

Phi = survival, f = recruitment, p = detection

Table 2. Ocelot estimated population size and density estimates obtained with non-spatial models, with standard error (SE) according to season, approach and MMDM.

Approach	Season	No. of Records	No. of Individuals	EPS -		\hat{p}	MMDM M	Density	Density	ETA	ETA	
				Estimated population size +/- SE	EPS LC			EPS UC	1 MMDM +/- SE	1/2 MMDM +/- SE	1 MMDM	1/2 MMDM
RA	Dry	30	21	54.5 +/- 12.7	37.3	89.9	0.0619	931	13.78 +/- 4.25	15.29 +/- 3.94	395	356
	Rainy	20	16	54.9 +/- 13.06	36.5	89.8	0.0442	-	-	-	-	-
	Dry + Rainy	50	31	114 +/- 20.9	82.5	166.5	0.0428	6006	12.55 +/- 8.17	19.48 +/-8.68	908	585
NRA	Dry	83	9	10.7 +/- 1.9	9.3	18.8	0.3372	1073	19.87 +/- 5.22	28.15 +/- 6.04	54	38
	Rainy	21	8	9 +/- 1.6	8	15.4	0.2083	1721	11.89 +/- 3.93	18.91 +/- 4.92	75	47
	Dry + Rainy	104	12	13.2 +/- 2.7	12.1	28.6	0.3592	939	26.47 +/- 7.49	36.39 +/- 8.64	36	49

Density is reported in ocelots per 100 km², MMDM is reported in meters, ETA is reported in km².

Table 3. Ocelot estimated population size and density estimates obtained with spatial models, with standard error (SE) according to season.

Approach	Season	Density +/- SE	Density LC	Density UC
RA	Dry	14.04 +/- 0.05	6.58	29.98
	Rainy	35.92 +/- 53.30	3.78	341.3
	Dry + Rainy	11.35 +/- NA	NA	NA
NRA	Dry	12.60 +/- 0.05	5.91	26.89
	Rainy	24.60 +/- 0.14	8.66	69.86
	Dry + Rainy	17.08 +/- 0.05	8.81	33.12

Density is reported in ocelots per 100 km²

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CAPÍTULO II – Manuscrito para submissão – Journal of Zoology

Activity patterns and temporal overlap with prey of a Neotropical felid assemblage in an Atlantic Forest protected area

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Abstract

Mammalian carnivores exert a significant influence on the ecosystem structure and functionality through the top-down control process. In addition to the influence on prey communities' composition, carnivores might also cause an impact on populations of other predators. In order to coexist, sympatric carnivores share resources, interacting in space and time. Carnivores' activity patterns usually coincide with the period that their prey is active and most vulnerable. Jaguars (*Panthera onca*), pumas (*Puma concolor*) and ocelots (*Leopardus pardalis*) are sympatric throughout an extensive portion of their distribution. Due mostly to habitat destruction, the Rio Doce State Park (RDPS) is one of the last patches of Atlantic forest where jaguars, pumas and ocelots are still sympatric. Several studies have described jaguars, pumas and ocelots activity patterns separately, but few have examined the ecological interactions between them at the same time and the same place and their prey simultaneously. In this study, we described these species activity patterns and quantified the temporal overlap between them and their potential prey. We obtained 11,078 independent records a total of 34 Vertebrate species were registered. Carnivores represented 9.4% of all records and prey species 90.6%. Jaguars accounted for 0.51% (57 records), pumas 1.91% (228 records) and ocelots 3.86% (428 records). In this study, jaguars, puma and ocelot females were classified as cathemeral, showing most significant activity during the day, while male pumas and male ocelots were classified as mostly nocturnal. We found a high temporal overlap between these three felid species (0.67 - 0.74). Regarding predator-prey activity period, felids overlapped extensively with their potential prey (0.60 – 0.83). The ecological knowledge acquired in this study

provided information regarding the temporal interactions of the three biggest felids in South America, since there was no previous knowledge about it in RDSP.

Key words: Camera trapping, Coexistence, *Leopardus pardalis*, *Panthera onca*, Predator, Prey, *Puma concolor*, Temporal partitioning

Introduction

Mammalian carnivores exert a significant influence on the ecosystem structure and functionality through the top-down control process (Steneck, 2005; Ritchie & Johnson, 2009; Wirsing *et al.*, 2017). In addition to the influence on prey communities composition, carnivores might also cause an impact on populations of other predators through mesopredator release (de Oliveira & Pereira, 2014; Pérez-Irineo & Santos-Moreno, 2016). In order to coexist, sympatric carnivores share resources, interacting in space and time (Schoener, 1974; Gordon, 2000). The coexistence among carnivores is influenced by body size, since larger species are able to exclude smaller ones from habitat patches or prey carcasses (Kamler *et al.*, 2003, 2012, 2015). In response to these interactions, smaller species may change the habitat use or alter their foraging behavior and activity patterns to diminish lethal encounters with dominant species (Kamler *et al.*, 2003, 2012, 2015; Elmhagen & Rushton, 2007; Ritchie & Johnson, 2009).

Regarding predator-prey interactions, predators, especially felids, hunt using their audition and vision primarily (Woolf, Sunquist & Sunquist, 2007; Silver *et al.*, 2009) and their activity patterns usually coincide with the period that their prey are active and most vulnerable. Thus, the species daily activity patterns assessment provides behavioral and ecological knowledge that may be interpreted as a measurement of energetic expenditure, foraging effort (Weckel, Giuliano & Silver, 2006) and predation risk (Kranstauber *et al.*, 2014).

The potential for competition among sympatric carnivore guilds results in a need for coexistence strategies. African carnivores such as the African wildcat (*Felis silvestris lybica*), grey mongoose (*Galerella pulverulenta*), small-spotted genet

(*Genetta genetta*), striped polecat (*Ictonyx striatus*), and the yellow mongoose (*Cynictis penicillata*), for example, co-occur based on a time partitioning behavior, separating into two temporal groups: nocturnal (wildcat, polecat and genet) and diurnal species (mongooses) (Satgé, Teichman & Cristescu, 2017). In the Neotropics, the jaguarundi may be strictly diurnal to reduce the effect of interference competition or attacks from the larger and mostly nocturnal species, like the ocelot, and also to minimize the competition with similar sized species, such as the margay through a temporal partitioning of their activities (Di Bitetti *et al.*, 2010).

Jaguars (*Panthera onca*), pumas (*Puma concolor*) and ocelots (*Leopardus pardalis*), the three largest felids in the Neotropics are sympatric throughout an extensive portion of their distribution (Emmons & Feer, 1997; Oliveira, 2002; IUCN, 2016). As most Neotropical carnivores, these felids have suffered major declines due to habitat loss and poaching, leading to their disappearance in large portions of their original distribution (Salom-Pérez *et al.*, 2007), especially in the Atlantic forest of South America (Beisiegel *et al.*, 2012; Paviolo *et al.*, 2016). Although originally covering approximately 139.584.893 hectares, currently only 16.377.472 ha (11.73%) of Atlantic Forest remains. The largest portion is distributed mostly in small fragments (< 100 ha) that are isolated from each other (Silva *et al.*, 2007; Ribeiro *et al.*, 2009). The Rio Doce State Park (RDPS) is one of the largest patches of the Atlantic forest where jaguars, pumas and ocelots are still sympatric (Viana, 2006; Keesen *et al.*, 2016), therefore RDSP plays an important role protecting a great diversity of medium and large sized mammals, among these several threatened species. However, accelerated change in land use around the reserve, environmental disasters like Mariana (Fernandes *et al.*, 2016; Omachi *et al.*, 2018) and Brumadinho dams collapse (Cionek *et al.*, 2019), human trespassing the

protected area and poaching may affect this realm of habitat and threaten the long-term survival of the wild felid assemblage in the region. Several prey species considered relevant for these cats' diet in the Atlantic forest biome are present in RDSP. For instance, the pecari (*Tayassu tajacu*), nine-banded armadillo (*Dasypus novemcinctus*) and brocket deer (*Mazama* spp.) are important prey for jaguars (Garla *et al.*, 2001; Azevedo, 2008; Foster, Harmsen & Doncaster, 2010). The South American coati (*Nasua nasua*), red-rumped agouti (*Dasyprocta azarae*) and paca (*Agouti paca*) are important prey for puma (Azevedo, 2008; Martins, Quadros & Mazzolli, 2008). The four-eyed opossum (*Metachirus nudicaudatus*), forest rabbit (*Sylvilagus brasiliensis*) and several small rodent species, are important resources for ocelots (Wang, 2003; Martins *et al.*, 2008; Rocha-Mendes *et al.*, 2011).

To increase the basic ecologic understanding of this Neotropical felid assemblage (Blake *et al.*, 2012), especially in the threatened Atlantic forest ecosystem information on how species coexist is important (e.g. activity patterns). Several studies have described jaguars, pumas and ocelots activity patterns separately, but few have examined the ecological interactions between them at the same time and the same place (Scognamillo *et al.*, 2003), and their prey simultaneously. In this study, we used camera-traps records to describe the activity patterns of jaguars, pumas and ocelots, and to quantify the temporal overlap between them and their potential prey species. In addition, we tested if there is a temporal segregation between sexes of each predator. We expected that jaguars, pumas and ocelots would segregate their daily activity patterns to minimize the probability of interspecific encounters. We also expected these three felid species would have a high degree of temporal overlap with their potential prey.

Materials and methods

Ethics statement

We used camera-traps in this study, which is a non-invasive technique that does not interfere with animal's behavior, as there is no direct contact. The research project was authorized by the competent local authority ICMBio/SISBIO, under research permits 93896765/2015-2016 and 54311277/2016-2017.

Study area

The Rio Doce State Park - RDSP is a conservation unit of integral protection in the state of Minas Gerais, southeastern Brazil (19°29' - 19°48' S / 42°28' - 42°38' W). The park covers an area of approximately 360 km², representing one of the largest continuous remnants of Atlantic Forest in Brazil and the largest in the state of Minas Gerais (Gontijo & Britto, 1997). Rio Doce State Park still holds populations of endangered and vulnerable carnivores species such as jaguar, puma, and jaguarundi (*Puma yagouaroundi*) (Machado, 1998; Pitman *et al.*, 2002; IUCN, 2016; Antonio De La Torre *et al.*, 2018). Considering the degree of fragmentation, RDSP represents an important area for the maintenance of biodiversity in the Atlantic Forest (Silva Júnior *et al.*, 2009). The vegetation is classified as "Submontane seasonal semideciduous forest" (IBGE, 2012). The climate of the region is classified as "humid subtropical", with two marked seasons: a rainy summer from October to March followed by a dry winter from April to September (Tundisi, 1997).

Sampling design

Sixty nine capture stations (a pair of camera-traps placed at a height of 40-50cm above the ground; Bushnell© Trophy Cam Natureview, Trophy Cam Standard and Trophy Cam Essential - Kansas, USA) were set to collect data to estimate

activity patterns of the mammal community in the RDSP.. Camera-traps were programmed to operate 24 hours/day, with an interval of 60 seconds between videos. No baits or any kind of attraction were used.

We positioned 54 capture stations randomly, covering the entire RDSP area. Due to logistical issues, we divided the area into two sectors: north and south, each including nine circular zones (buffers) with 2.5 km in diameter, which represent the smaller known home-range for female jaguars (initial target-species for an abundance/density study). In each buffer, three locations were determined randomly for installing camera-traps (Figure 1), totalizing 27 stations per sector (54 total), with minimum distance of 1.3 km between stations. This experiment lasted a period of 11 months, comprehending dry (from April to August 2016) and wet (from November 2016 to March 2017) seasons.

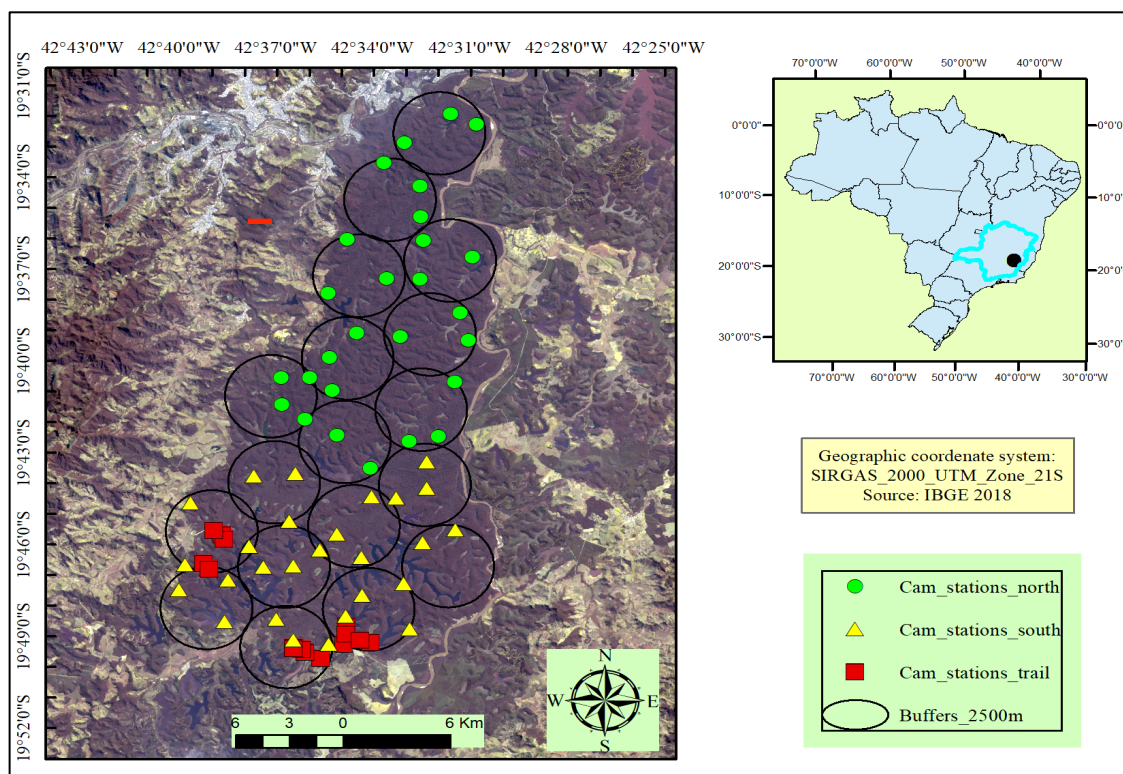


Figure 1. Distribution of buffers and camera-trap stations in Rio Doce State Park. Black circles indicate 2,5km buffers; green circles and yellow triangles represent stations installed randomly in North and South sectors of the park, respectively; red squares represent stations installed in roads.

Additionally, from April 2017 to November 2018, 15 stations were installed along low-traffic (<1 vehicle/day) unpaved roads, used exclusively for research and maintenance in the southern sector of RDSP (Fig. 1). Locations of stations were determined to maximize the capture probability of carnivores, selecting sites with evidences of their presence, such as tracks, scraps and scats.

Camera-trap surveys were carried out during consecutive years and apparently no significant biological, environmental or anthropogenic changes happened in the area during the study period, therefore through pooling records from multiple years, we assumed that detection and activity patterns of all species were similar along studied years.

Data analysis

All registers obtained were cataloged in a database containing species, date, hour and capture station location. To avoid spatial pseudo-replication, camera-traps less than 500 m apart were considered as a single capture station. Records of species detected at the same capture station were considered as independent when in a 30 minutes interval (Ridout & Linkie, 2009; Linkie & Ridout, 2011). Considering this same interval, multiple individuals of the same species were considered as one single record of the species (Azevedo *et al.*, 2018). Predator and prey species activity pattern was determined comparing the proportion of daily (from sunrise to sunset), and nocturnal records (from sunset to sunrise) (Griffiths & van Schaik, 1993). The successive changes of sun's position throughout the year were considered, adjusting the specific sunrise time for each record (or sunset time for night records), setting sunrise and sunset to $\pi/2$ and $3\pi/2$, respectively (Nouvellet *et al.*, 2012). Attending a prerequisite to perform the activity classification, only species

with more than 45 records (Gómez *et al.*, 2005) were classified as diurnal if (<10% of records at night), nocturnal ($\geq 90\%$ of records at night), mostly diurnal (10–29% of records at night), mostly nocturnal (70–89% of records at night), or cathemeral (30–69% of records at night) (Gómez *et al.*, 2005). For each species, daily activity patterns were assessed using a non-parametric circular kernel-density function. The overlap between predators and their prey was measured through a coefficient of overlapping, taking the minimum of the density functions from two sets of samples being compared at each point in time. Overlap coefficient ranged from 0 (no overlap) to 1 (complete overlap) (Ridout & Linkie, 2009; Linkie & Ridout, 2011). The 95% confidence intervals of each overlap index were calculated using smoothed bootstrap with 10,000 resamples (Meredith & Ridout, 2017). All analyses were performed in R environment v.1.1.463 (R Core team, 2017) using the ‘overlap’ R-package (Meredith & Ridout, 2017). A quasi-Poisson distribution was used to account for overdispersion in the count data (records per hour) (Breslow, 1990). To detect differences in activity patterns accordingly to sex, for predator species with more than 45 records/sex, we tested separately male and female overlap with the other felids and with their potential prey (Azevedo *et al.*, 2018), which were determined considering species cited as relevant in each predator diet in the Atlantic Forest. Only prey species with more than 45 independent records were considered.

Results

We obtained 11,078 independent records, with a total effort of 6,618 trap-nights (Table S1). Carnivore species represented 9.4% (1,040 records) of all records and prey species 90.6% (10,038 records). Jaguars accounted for 0.51% (n = 57; 18 records for males, six for females and 33 for unidentified sex), pumas 1.91% (n = 212; 59 records for males, 127 for females and 26 for unidentified sex), and ocelots 3.86% (n = 428; 147 records for males, 37 for females and 244 for unidentified sex). Other wild carnivores represented 2.79% (309 records) and exotic carnivores (*Canis lupus familiaris* and *Felis catus*) 0.16% (18 records) (Table 1).

Table 1. Number of independent records per species obtained by camera-traps at Rio Doce State Park, between 2016 and 2017. per species

Species*	Records
Birds*	3,539
<i>Cabassous tatouay</i>	22
<i>Caiman latirostris</i>	3
<i>Canis familiaris</i>	17
<i>Cerdocyon thous</i>	45
<i>Chrysocyon brachyurus</i>	3
<i>Coendou prehensilis</i>	1
<i>Cuniculus paca</i>	123
<i>Dasyprocta leporina</i>	1,545
<i>Dasypus novemcinctus</i>	592
<i>Didelphis sp.</i>	605
<i>Eira barbara</i>	138
<i>Euphractus sexcinctus</i>	1
<i>Felis domesticus</i>	1
<i>Puma yagouaroundi</i>	19
<i>Hydrochaeris hydrochaeris</i>	199
<i>Leopardus pardalis</i>	428

<i>Lontra longicaudis</i>	1
<i>Mazama</i> sp.	166
<i>Metachirus nudicaudatus</i>	121
<i>Nasua nasua</i>	100
<i>Panthera onca</i>	57
<i>Pecari tajacu</i>	322
<i>Priodontes maximus</i>	88
<i>Procyon cancrivorous</i>	3
<i>Puma concolor</i>	228
Rodents*	146
<i>Salvator merianae</i>	481
<i>Sapajus</i> sp.	25
<i>Sus scrofa</i>	1
<i>Sciurus ingrami</i>	72
<i>Sylvilagus brasiliensis</i>	631
<i>Tamandua tetradactyla</i>	47
<i>Tapirus terrestris</i>	1,304
TOTAL	11,074

*Birds and small-sized rodents could not be identified at species level and were considered as one group.

At total, 34 Vertebrate species were registered at camera-trap stations. From these, the number of records for each species (>45) allowed us to determine the activity pattern for 20 of the 34 registered (not considering birds and small-sized rodents (Table 2). Ocelot was the most registered carnivore species (n=428), followed by pumas (n=228), tayras (*Eira barbara*, n=138) and coatis (n=100).

Table 2. Classification of activity period of three medium- and large sized wild felids and their main prey at Rio Doce State Park.

Species	N	Diurnal records (%)	Nocturnal records (%)	Activity Pattern
<i>Panthera onca</i>	57	35.1	64.9	catheMERal
<i>Puma concolor</i> male	58	41.4	58.6	catheMERal
<i>Puma concolor</i> female	128	18.7	81.3	catheMERal
<i>Leopardus pardalis</i> male	147	24.5	75.5	mostly nocturnal
<i>Leopardus pardalis</i> female	47	37.8	62.2	catheMERal
<i>Cerdocyon thous</i>	45	31.1	68.9	catheMERal
<i>Eira barbara</i>	138	92	8	diurnal
<i>Nasua nasua</i>	100	88	12	mostly diurnal
<i>Pecari tajacu</i>	322	78.6	21.4	mostly diurnal
<i>Cuniculus paca</i>	123	0	100	nocturnal
<i>Dasyprocta leporina</i>	1545	90.3	9.7	diurnal
<i>Dasypus novemcinctus</i>	592	2.7	97.3	nocturnal
<i>Mazama</i> sp.	166	21.7	78.3	mostly nocturnal
<i>Didelphis</i> sp.	605	1.8	98.2	nocturnal
<i>Metachirus nudicaudatus</i>	121	1.7	98.3	nocturnal
Small-sized Rodents	146	2.1	97.9	nocturnal
<i>Hydrochoerus hydrochaeris</i>	199	51.3	48.7	catheMERal
<i>Sciurus ingrami</i>	72	90.3	9.7	diurnal
<i>Sylvilagus brasiliensis</i>	631	3	97	nocturnal
<i>Tamandua tetradactyla</i>	47	6.4	93.6	nocturnal
<i>Salvator merianae</i>	481	99.4	0.6	diurnal
Birds	3539	85.9	14.1	mostly diurnal

For jaguars, the number of records was not statistically sufficient to test for differences in activity period among sexes (Figure 2). Thus, independently of sexes, jaguar behavior was classified as catheMERal. In general, pumas were catheMERal, but differed in activity patterns during the day and night hours. Males did not present different activity patterns between periods of day, being 1.4 times more active during night than daytime hours (average of 2.83 records per hour during the night and 2.0 during the day) (Figure 2). Females differed in activity patterns between periods of day, being 1.7 times more active during day than nighttime hours (average of 4.0 records per hour during the night and 6.67 during the day) (Figure 2, 3).

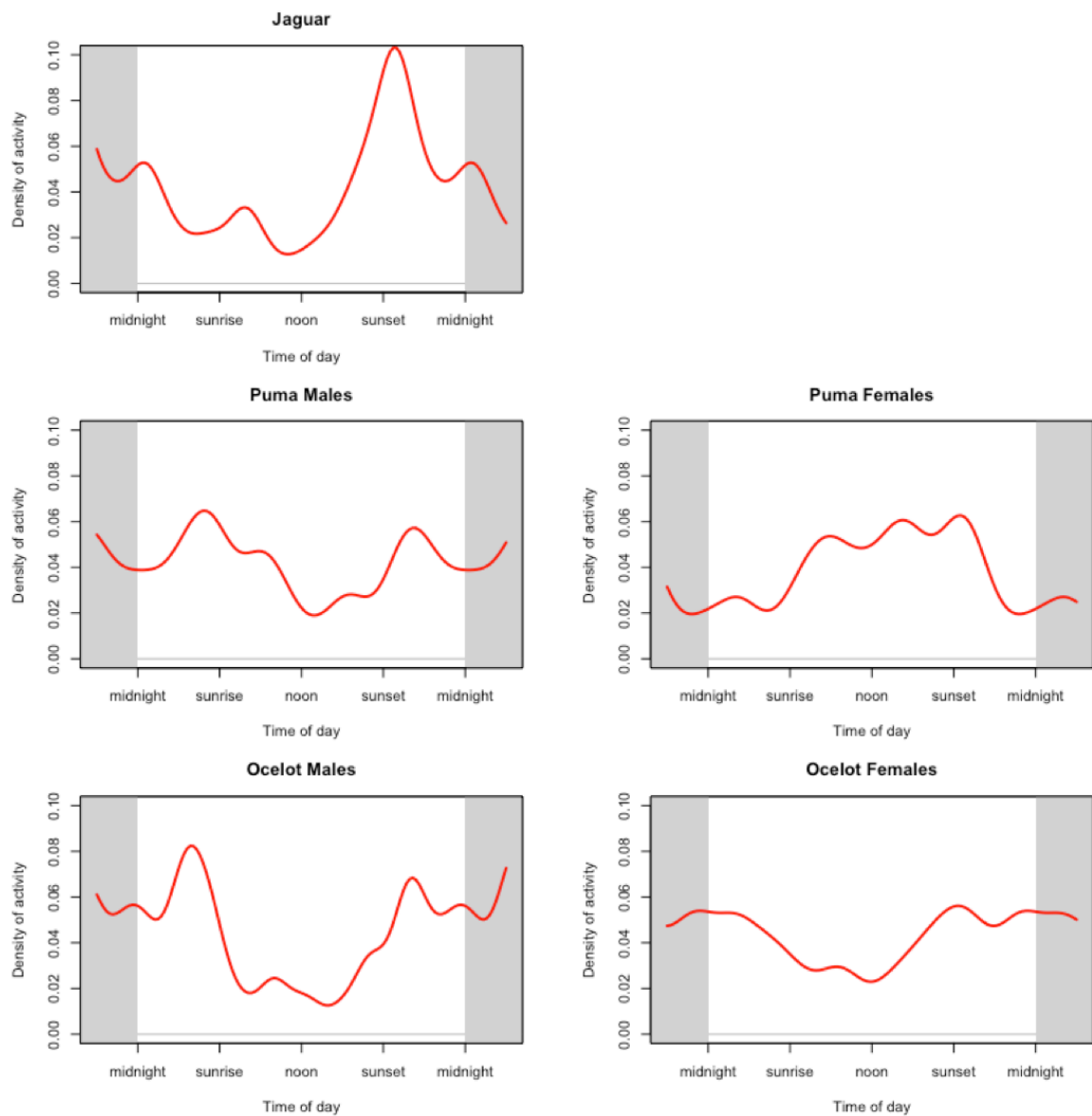


Figure 2. Activity patterns of jaguars, pumas and ocelots at Rio Doce State Park.

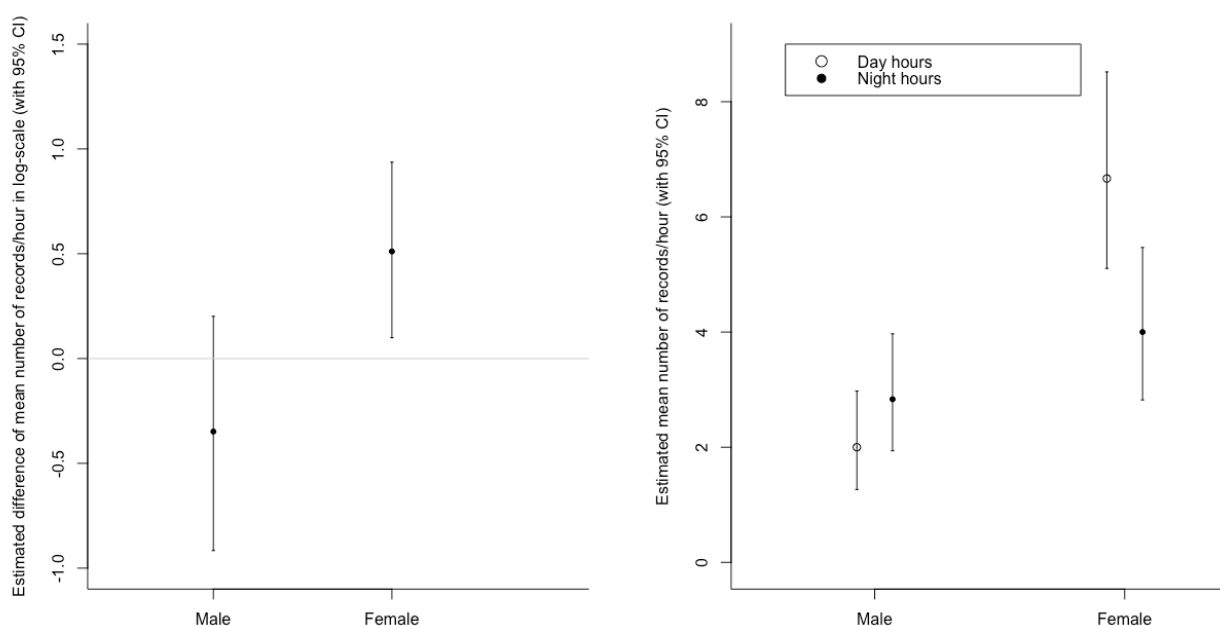


Figure 3. Estimated mean and difference of mean (Day-Night) number of records between puma males and females with confidence intervals.

Ocelots differed in activity patterns during the day and night hours. Male ocelots were mostly nocturnal and females were cathemeral. Males presented different activity patterns between periods of day, being 3.1 times more active during night than daytime hours (average of 9.25 records per hour during the night and 3.0 during the day). Females did not differ in activity patterns between periods of day, being 1.6 times more active during night than daytime hours (average of 1.91 records during the night and 1.17 during the day) (Figure 2, 4).

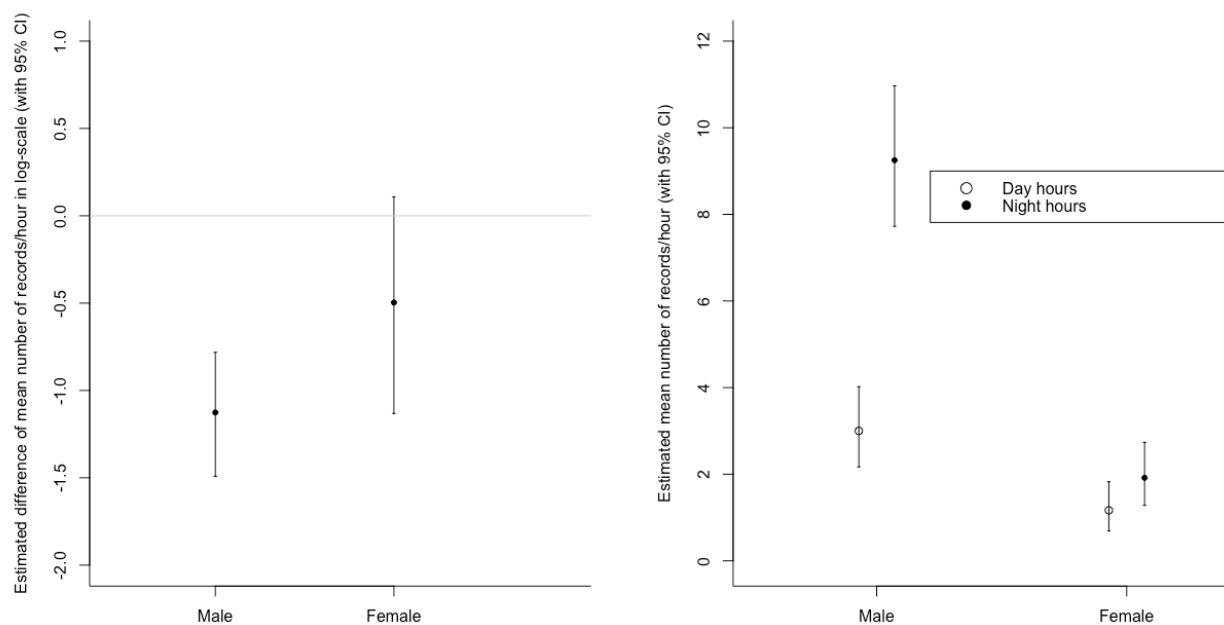


Figure 4. Estimated mean and difference of mean (Day-Night) number of records between ocelot males and females with confidence intervals.

Jaguars showed a high temporal overlap between both male (0.72, CI – 0.57 – 0.85) and female pumas (0.72, CI – 0.60 – 0.84) and also with ocelots (0.74, CI = 0.63 - 0.85). Puma males showed a higher overlap with ocelots (0.80, CI – 0.70 – 0.90) than females (0.59, CI – 0.51 – 0.67) (Figure 5) (Tables S1, S2, S3).

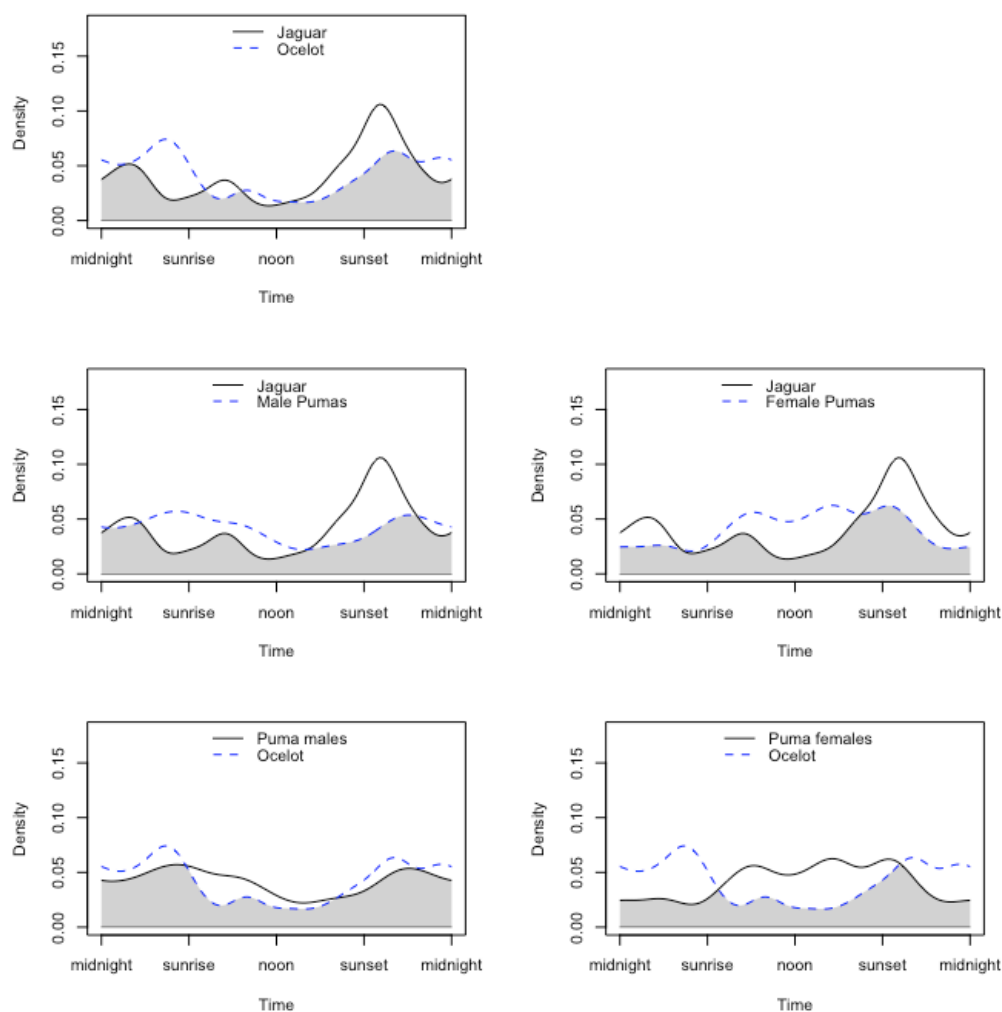


Figure 5. Overlap index between large- and medium-sized felids at Rio Doce State Park.

Regarding predator-prey activity period overlap, jaguars overlapped extensively with some of their potential prey (Table S2), such as capybara (*Hydrochaerus hydrochaeris* – 0.79, CI=0.69 - 0.89), brocket deer (*Mazama* sp. – 0.77, CI = 0.65 - 0.87), tapir (*Tapirus terrestris* – 0.76, CI = 0.65 - 0.87), and collared-peccary (*Pecari tajacu* – 0.60, CI = 0.48 - 0.71) (Table S2) (Figure 6). Among their potential prey, pumas had higher overlap with capybara (0.83, CI = 0.76 - 0.91), collared-peccary (0.78, CI = 0.71 - 0.85), coati (*Nasua nasua* – 0.69, CI = 0.61 - 0.77) and agouti (*Dasyprocta leporina* – 0.63, CI = 0.58 - 0.92). Male pumas overlapped extensively with capybaras (0.85, CI = 0.76 - 0.92), collared-

peccary (0.85, CI = 0.78 - 0.92), brocket deer (0.67, CI = 0.55 - 0.79) and nine-banded armadillo (0.55, CI = 0.44 - 0.67)) (Table S3) (Figure 7). Female pumas also showed high overlap with capybaras (0.85, CI = 0.76 - 0.92) and collared-peccary (0.85, CI = 0.78-0.92), but also with South American coatis (0.75, CI = 0.65 - 0.84) and agoutis (0.68, CI = 0.60 - 0.74) (Figure 8). Ocelots overlapped more extensively with brown four-eyed opossums (*Metachirus nudicaudatus* – 0.77, CI = 0.70 - 0.82), small-sized rodents (0.75, CI = 0.69-0.80), tapeti (*Sylvilagus brasiliensis*) (0.72, CI = 0.67 - 0.76) and big-eared opossum (0.72, CI = 0.67 - 0.77) (Table S4) (Figure 9).

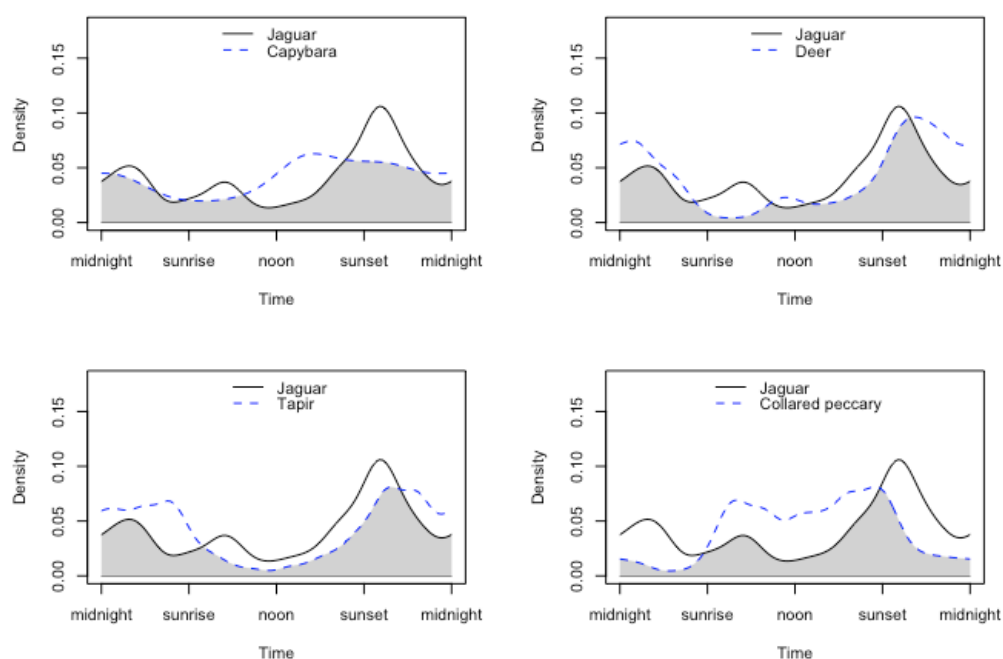


Figure 6. Overlap index between jaguars and their potential main prey at Rio Doce State Park.

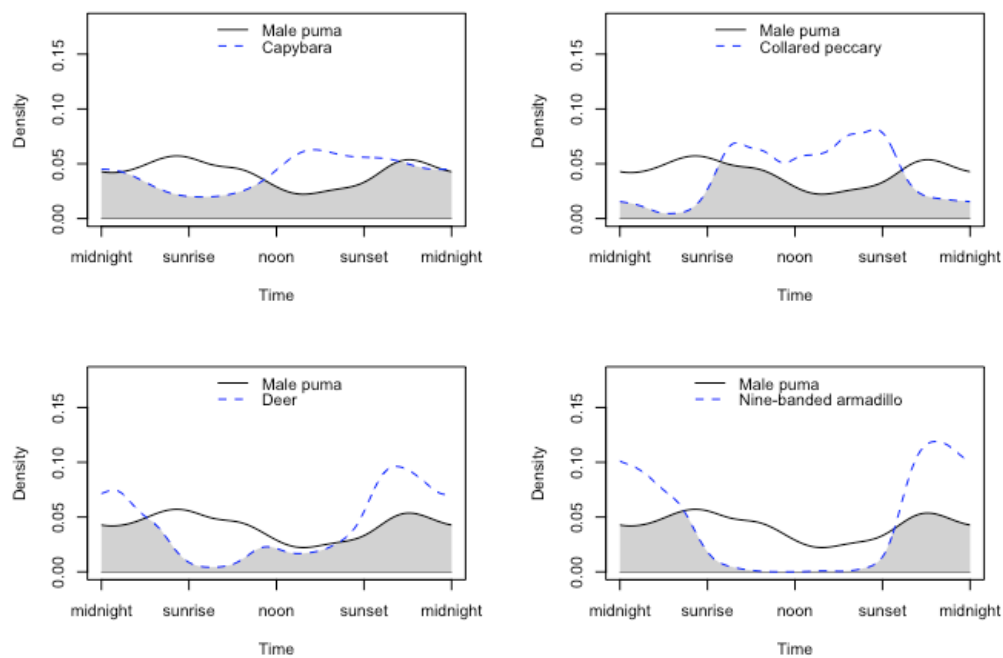


Figure 7. Overlap index between male pumas and their potential main prey at Rio Doce State Park.

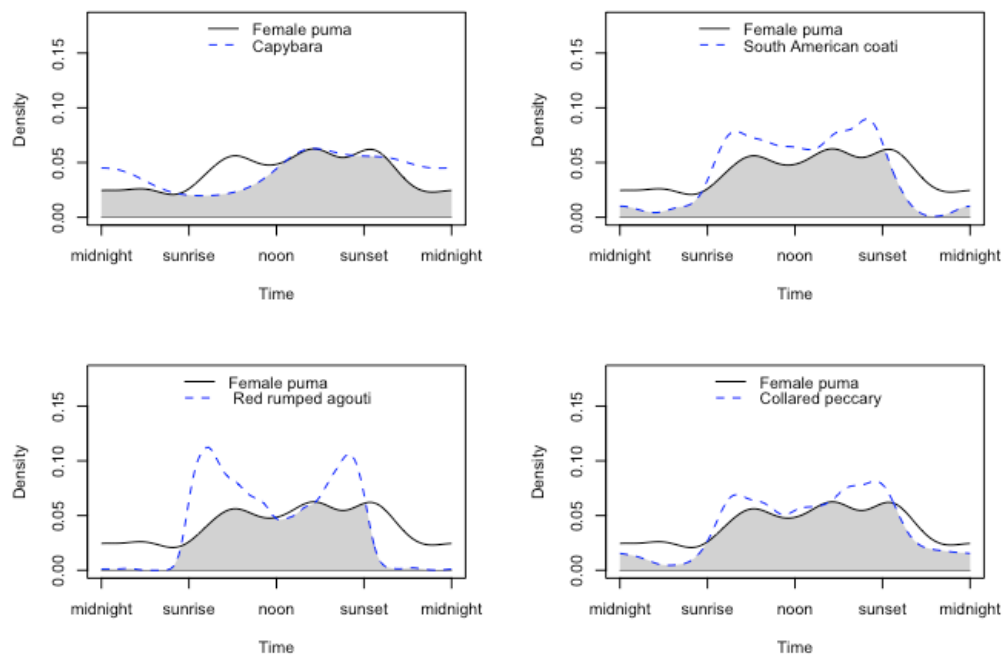


Figure 8. Overlap index between female pumas and their potential main prey at Rio Doce State Park.

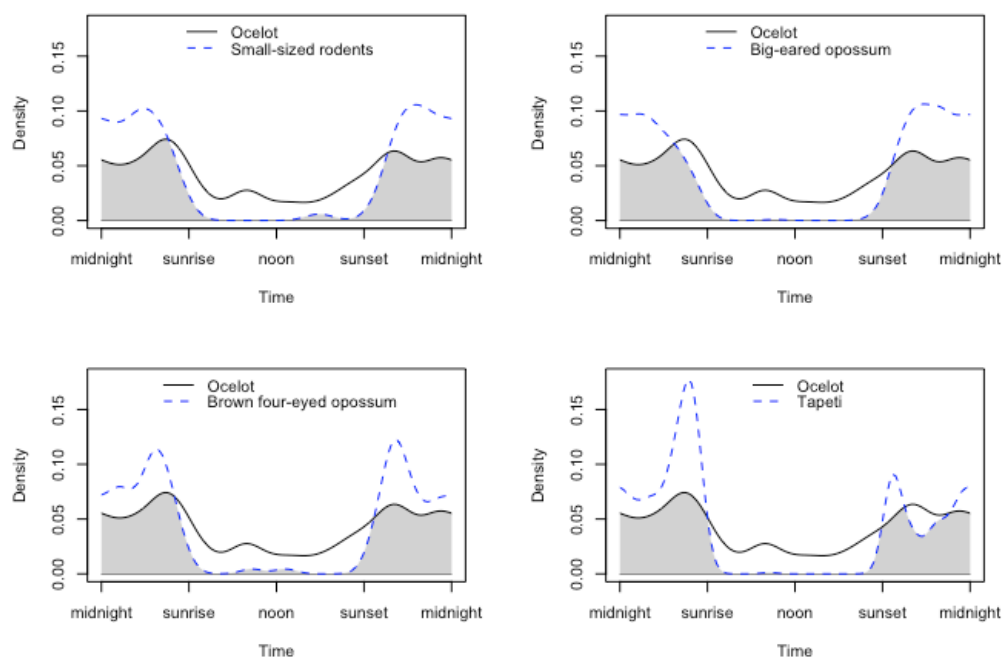


Figure 9. Overlap index between ocelots and their potential main prey at Rio Doce State Park.

Discussion

The majority of previous studies that used camera traps to evaluate activity patterns considered only a relatively short period of sampling (Blake *et al.*, 2012). Many species show annual variation in their activity patterns, therefore long-term studies are recommended to fully evaluate patterns of activity of Neotropical mammals (Blake *et al.*, 2012). In our study, the 11 months of data collection allowed the detection of several different species and their seasonal variations in activity periods throughout the years. Nevertheless, from the 3 selected felid species, pumas and ocelots were sufficiently common to evaluate males and females separately and determine their activity patterns. Likewise in other Neotropical areas, ocelot was the most frequent carnivore species registered in our study (Cuellar *et al.*, 2006; de Oliveira & Pereira, 2014). For other carnivores, such as jaguarondi, crab-eating racoon (*Procyon cancrivorus*), Neotropical otter

(*Lontra longicaudis*) and maned-wolf (*Chrysocyon brachyurus*), the low number of records made impossible to estimate patterns of activity, probably due to their rarity in this environment.

In theory, the coexistence of carnivore species is possible because of their difference in size, morphology or behavior (Rosenzweig, 1966; Pianka, 1974). Species daily activity varies over time and space, indicating that multiple factors probably interact determining patterns of activity. The high temporal overlap among these three predators showed by our results suggests that other factors, such as the high diversity and availability of prey, may be involved in this assemblage coexistence. The temporal segregation that generally occurs among sympatric carnivores may be a strategy to minimize interference competition and consequently, the risk of intraguild predation (Fedriani *et al.*, 2000). This segregation pattern however, is not frequently reported for large-sized predators like jaguars and pumas (Romero-Muñoz *et al.*, 2010).

In our study, jaguars, puma and ocelot females were classified as cathemeral, showing most significant activity during the day, while male pumas and male ocelots were classified as mostly nocturnal, an activity pattern extensively recorded for the species (Emmons & Feer, 1997; Massara *et al.*, 2016; Santos *et al.*, 2019). Although the cathemeral behavior is not frequently reported for jaguars (Hernández-Saintmartín *et al.*, 2013), it has been reported in Amazonia (Emmons, 1987; Gómez *et al.*, 2005), subtropical forests of Mexico (Hernández-Saintmartín *et al.*, 2013), Venezuelan llanos (Scognamillo *et al.*, 2003), and recently in the Caatinga, Cerrado and Cerrado/Amazonia ecotone in Brazil (Foster *et al.*, 2013). For pumas, this behavior is more common and has been often reported (Harmsen *et al.*, 2009; Di Bitetti *et al.*, 2010; Azevedo *et al.*, 2018).

The cathemeral behavior could be specifically beneficial for generalist predators which consume a broader variety of prey, including diurnal and nocturnal species (Oliveira, 2002), since it increases the encounter probability with a more diverse prey spectrum (Scognamillo *et al.*, 2003). That may be the case for jaguars and female pumas and ocelots in RDSP. Moreover, the RDSP is quite remote, surrounded by the Doce River on the eastern border and with few roads within its borders. Because diurnal activity of large felids can be an indicator of low human disturbance in the habitat (Paviolo *et al.*, 2009), this remoteness may contribute to minimal human presence inside the protected area, favoring jaguars and pumas to be more active during daylight.

Contrary to our expectation that jaguars, pumas and ocelots would segregate their daily activity patterns to minimize the probability of encounters, we found a high overlap index between these three felids. Despite the large effort, the low number of jaguar records suggests that this species occurs in low numbers in the region, thus may not affect the temporal activity of smaller felids in the RDSP. Similar results were observed in areas where jaguars are virtually absent and smaller species may extend their diurnal activity (Paviolo *et al.*, 2009; Santos *et al.*, 2019).

As expected, jaguars and ocelots did not show differences in their activity patterns accordingly to sex. On the other hand, contrary to our expectation and differently from other studies (Romero-Muñoz *et al.*, 2010), this difference was observed for pumas, as our results showed that females were considerably more activity during the day than during the night, while males showed more nocturnal activity. This behavior can be justified by an attempt of females to avoid males, since these encounters may result in agonistic events (Logan & Swenar, 2001;

Harmsen *et al.*, 2009; Azevedo *et al.*, 2018). However, recent studies provided evidence that pumas, a non-cooperative solitary species, associate with conspecifics with regularity (Elbroch & Quigley, 2017) suggesting that pumas may be more social than earlier research evaluated. Despite of displaying different activity patterns, pumas showed an extensive overlap between males and females. In addition, we observed a series of intra-specific interactions (unpublished data) as documented in other protected areas with a large and broad prey availability (Elbroch & Quigley, 2017).

In favor of our expectation that the three selected felid species would show a high temporal overlap with their potential prey, our results reinforce the idea that activity patterns of Neotropical felids are determined by prey availability (Emmons, 1987; Núñez, Miller & Lindzey, 2000; Scognamillo *et al.*, 2003; Harmsen *et al.*, 2011). Although no studies determining jaguar's preferred prey at RDSP were conducted, we found high temporal overlap between jaguars and some of potential prey species for this predator in the Atlantic forest (Garla *et al.*, 2001; Novack *et al.*, 2005; Foster *et al.*, 2010). The diversity of prey in RDSP may explain the narrow overlap found between jaguars and other potential prey species in RDSP, like South American coati and agouti (*Dasyprocta leporina*) (Garla *et al.*, 2001). For pumas, as they showed diverse activity patterns accordingly to sex, males showed a mostly nocturnal behavior, avoiding the warmest hours of the day. This behavior may reflect a diet based on a narrower roll of mostly nocturnal prey such as four-eyed opossum, big-eared opossum, forest rabbit or even larger prey like southern tamandua and brocket deer. In the RDSP, male pumas weight up almost two times than females (unpublished data). In addition, this temporal segregation between sexes may be an indication that

females feed on different prey than males, being active for a longer period in order to encounter a broader variety of prey, from the mostly nocturnal brocket deer, to the mostly diurnal collared-peccary. This diurnal activity of females may also reflect a preference for diurnal prey species, such as tegus and coatis. Both jaguars and pumas showed an extensive overlap with giant-armadillo (*Priodontes maximus*), nevertheless this species had never been reported as a relevant prey for neither predator, probably because it usually occurs in low densities (Aguiar & da Fonseca, 2008). The high overlap found between ocelots and their potential prey also suggest that prey is a key factor determining this species activity patterns. For instance, ocelots also overlapped extensively with some of their most important prey in the Atlantic Forest, as the tapeti, small rodents, four-eyed opossum and big-eared opossum.

The ecological knowledge acquired in our study, provided information regarding the use of time by the three biggest felids in South America and their prey and can be considered fundamental to better understand how community composition may influence species activity patterns. There are few studies providing information about daily activity of multiple species from the same location (Gómez *et al.*, 2005; Weckel *et al.*, 2006; Tobler, Carrillo-Percestequi & Powell, 2009; Blake *et al.*, 2012). We recommend further studies to focus habitat use and prey consumption by these felids in RDSP to better understand the interaction between them and their prey.

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Table S1. Jaguar overlap index with lower and upper confidence intervals of prey and other predators at Rio Doce State Park.

	Jaguar	LCI	UCI	Males	LCI	UCI	Females	LCI	UCI
<i>Hydrochoerus hydrochaeris</i>	0.799	0.693	0.898	0.723	0.543	0.885	0.443	0.193	0.676
<i>Mazama</i> sp.	0.773	0.654	0.878	0.744	0.580	0.902	0.379	0.146	0.57
<i>Tapirus terrestris</i>	0.769	0.651	0.871	0.745	0.567	0.898	0.447	0.242	0.655
<i>Leopardus pardalis</i>	0.743	0.630	0.853	0.739	0.546	0.900	0.379	0.172	0.589
<i>Puma concolor</i>	0.736	0.609	0.850	0.722	0.546	0.880	0.482	0.254	0.707
<i>Pecari tajacu</i>	0.605	0.485	0.718	0.604	0.413	0.777	0.481	0.248	0.7
<i>Dasypus novemcinctus</i>	0.594	0.469	0.716	0.571	0.387	0.742	0.272	0.069	0.476
<i>Metachirus nudicaudatus</i>	0.591	0.475	0.701	0.573	0.392	0.760	0.315	0.078	0.551
<i>Didelphis</i> sp.	0.589	0.471	0.703	0.564	0.377	0.736	0.276	0.078	0.485
<i>Cuniculus paca</i>	0.560	0.422	0.684	0.544	0.335	0.735	0.246	0.047	0.451
<i>Sylvilagus brasiliensis</i>	0.560	0.449	0.663	0.597	0.405	0.764	0.354	0.182	0.589
<i>Cerdocyon thous</i>	0.553	0.395	0.705	0.594	0.399	0.800	0.336	0.107	0.611
<i>Priodontes maximus</i>	0.535	0.397	0.671	0.546	0.334	0.739	0.213	0.031	0.433
Small-sized Rodents	0.524	0.410	0.654	0.517	0.322	0.708	0.243	0.053	0.461
<i>Nasua nasua</i>	0.499	0.372	0.634	0.508	0.312	0.699	0.459	0.207	0.697
<i>Tamandua tetradactyla</i>	0.485	0.339	0.629	0.548	0.335	0.760	0.246	0.060	0.487
Birds	0.469	0.368	0.577	0.470	0.282	0.669	0.410	0.181	0.649
<i>Dasyprocta leporina</i>	0.430	0.319	0.541	0.440	0.241	0.638	0.465	0.215	0.689
<i>Eira barbara</i>	0.407	0.293	0.536	0.401	0.192	0.601	0.347	0.142	0.56
<i>Sciurus ingrami</i>	0.266	0.158	0.384	0.305	0.116	0.498	0.187	0.020	0.43
<i>Salvator merianae</i>	0.225	0.136	0.319	0.223	0.066	0.397	0.190	0.008	0.44

Table S2. Puma overlap index with lower and upper confidence intervals of prey and other predators at Rio Doce State Park.

	Puma	LCI	UCI	Males	LCI	UCI	Females	LCI	UCI
<i>Hydrochoerus hydrochaeris</i>	0.838	0.769	0.910	0.729	0.610	0.835	0.858	0.768	0.926
<i>Pecari tajacu</i>	0.787	0.719	0.854	0.607	0.490	0.724	0.853	0.785	0.921
<i>Panthera onca</i>	0.736	0.610	0.847	0.725	0.578	0.850	0.722	0.607	0.841
<i>Nasua nasua</i>	0.698	0.613	0.777	0.527	0.405	0.654	0.757	0.657	0.844
Birds	0.685	0.624	0.741	0.544	0.424	0.662	0.733	0.656	0.8
<i>Leopardus pardalis</i>	0.676	0.605	0.743	0.808	0.704	0.900	0.599	0.514	0.678
<i>Tapirus terrestris</i>	0.657	0.596	0.718	0.771	0.660	0.872	0.587	0.509	0.665
<i>Dasyprocta leporina</i>	0.638	0.582	0.692	0.495	0.375	0.613	0.682	0.609	0.747
<i>Eira barbara</i>	0.634	0.561	0.709	0.495	0.370	0.625	0.677	0.587	0.764
<i>Mazama sp.</i>	0.618	0.532	0.698	0.674	0.556	0.799	0.580	0.482	0.672
<i>Cerdocyon thous</i>	0.583	0.469	0.689	0.711	0.556	0.837	0.508	0.386	0.623
<i>Priodontes maximus</i>	0.473	0.391	0.559	0.632	0.510	0.758	0.391	0.297	0.488
<i>Sylvilagus brasiliensis</i>	0.464	0.409	0.520	0.593	0.480	0.698	0.399	0.321	0.47
<i>Tamandua tetradactyla</i>	0.457	0.350	0.570	0.613	0.468	0.751	0.381	0.270	0.494
<i>Metachirus nudicaudatus</i>	0.455	0.388	0.516	0.602	0.481	0.719	0.378	0.297	0.458
<i>Dasypus novemcinctus</i>	0.449	0.389	0.508	0.555	0.442	0.676	0.388	0.312	0.46
<i>Sciurus ingrami</i>	0.445	0.358	0.536	0.442	0.313	0.565	0.452	0.350	0.559
<i>Didelphis sp.</i>	0.438	0.381	0.499	0.548	0.434	0.668	0.375	0.304	0.45
<i>Cuniculus paca</i>	0.428	0.363	0.495	0.551	0.437	0.672	0.362	0.284	0.447
Small-sized Rodents	0.427	0.366	0.499	0.589	0.468	0.702	0.347	0.272	0.432
<i>Salvator merianae</i>	0.414	0.354	0.473	0.288	0.189	0.389	0.467	0.385	0.543

Table S3. Ocelot overlap index with lower and upper confidence intervals of prey and other predators at Rio Doce State Park.

	Ocelot	LCI	UCI	Males	LCI	UCI	Females	LCI	UCI
<i>Tapirus terrestris</i>	0.905	0.866	0.938	0.872	0.802	0.933	0.820	0.697	0.927
<i>Mazama</i> sp.	0.808	0.745	0.867	0.758	0.675	0.837	0.769	0.630	0.894
<i>Priodontes maximus</i>	0.776	0.691	0.853	0.735	0.632	0.830	0.638	0.489	0.79
<i>Metachirus nudicaudatus</i>	0.770	0.708	0.825	0.733	0.647	0.813	0.614	0.472	0.746
Small-sized Rodents	0.751	0.690	0.804	0.710	0.630	0.787	0.595	0.447	0.742
<i>Panthera onca</i>	0.743	0.628	0.845	0.739	0.612	0.845	0.821	0.672	0.947
<i>Cuniculus paca</i>	0.735	0.678	0.791	0.676	0.597	0.756	0.596	0.457	0.747
<i>Sylvilagus brasiliensis</i>	0.721	0.673	0.767	0.713	0.652	0.776	0.633	0.515	0.747
<i>Dasypus novemcinctus</i>	0.720	0.670	0.766	0.656	0.578	0.728	0.610	0.470	0.741
<i>Didelphis</i> sp.	0.720	0.671	0.770	0.656	0.583	0.734	0.603	0.451	0.735
<i>Hydrochoerus hydrochaeris</i>	0.712	0.641	0.775	0.718	0.639	0.799	0.836	0.697	0.954
<i>Tamandua tetradactyla</i>	0.687	0.565	0.805	0.709	0.577	0.831	0.604	0.424	0.767
<i>Cerdocyon thous</i>	0.681	0.562	0.799	0.713	0.584	0.830	0.627	0.459	0.787
<i>Puma concolor</i>	0.676	0.608	0.751	0.694	0.609	0.785	0.828	0.699	0.944
<i>Pecari tajacu</i>	0.457	0.399	0.519	0.478	0.402	0.560	0.621	0.489	0.752
Birds	0.372	0.332	0.412	0.411	0.343	0.484	0.518	0.373	0.659
<i>Nasua nasua</i>	0.371	0.299	0.448	0.399	0.307	0.496	0.534	0.382	0.675
<i>Eira barbara</i>	0.323	0.259	0.387	0.360	0.277	0.446	0.464	0.328	0.613
<i>Dasyprocta leporina</i>	0.321	0.281	0.361	0.361	0.289	0.435	0.474	0.338	0.62
<i>Sciurus ingrami</i>	0.267	0.205	0.338	0.298	0.218	0.386	0.331	0.199	0.478
<i>Salvator merianae</i>	0.179	0.140	0.217	0.186	0.129	0.246	0.278	0.156	0.409

CAPÍTULO III – Manuscrito para submissão – Journal of Mammalogy

Spatial ecology and habitat selection by jaguars and pumas in a protected area in the Atlantic Forest of Brazil

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ABSTRACT

The knowledge about how animals are distributed is important to understand natural history, population dynamics, inter and intraspecific interactions. This information is useful to plan and evaluate management and conservation strategies, especially for scarce and threatened species occurring sympatrically such as jaguars (*Panthera onca*) and pumas (*Puma concolor*). Significant advances in understanding jaguar and puma ecology in tropical ecosystems were made in the past years, but information on the spatial ecology still lacks in most of their distribution, particularly in the Atlantic forest. The Rio Doce State Park (RDPS) is one the largest patches of the Atlantic forest where jaguars and pumas are still sympatric. The focus of this study was to describe and compare the spatial ecology of jaguars and pumas in the RDSP. We used GPS-collars to estimate home ranges, overlap between monitored individuals and evaluate habitat use and selection. We monitored two jaguars (one male and one female) and five pumas (two males and three females). Both jaguars and pumas showed high overlap and selection for natural habitats, such as forest and water; and avoidance of anthropic habitats, like urban areas and agriculture. Our results emphasize the importance of maintaining large natural areas for jaguars and pumas in the Atlantic Forest in order to maintain long-term population viability (genetically and demographically).

KEY WORDS

Coexistence, Global Positioning System, Home range, Overlap, *Panthera onca*, *Puma concolor*, Rio Doce State Park

INTRODUCTION

In order to meet daily requirements, carnivores usually occupy large areas and use specific habitat types and resources during different phases of their life time (Nowell and Jackson 1996; Morato et al. 2016). To reach important resources and expend less energy, animals may develop cognitive maps of their territory, recording the location and the path to these resources (Powell 2012; Spencer 2012). Therefore, the knowledge about how carnivores distribute themselves in the landscape is important to understand natural history, population dynamics, inter and intraspecific interactions and the mechanisms that promote survival and reproduction (Phillips et al. 2005; Gonzalez-Borrajo et al. 2017; Azevedo et al. 2019). These informations are essential to plan and evaluate management and conservation strategies (Coppolillo et al. 2004; Haines et al. 2006; Karanth et al. 2011), especially for scarce and threatened species (Quigley and Crawshaw 1992; López-Bao et al. 2010) such as the largest felids found in the Neotropics, the jaguar (*Panthera onca*) and the puma (*Puma concolor*). Both species have broad distribution, occupy diverse habitat types (Sanderson et al. 2002) and occur sympatrically throughout most of their geographic range (Emmons and Feer 1997). As for most of the large carnivore species, their populations are declining, due to habitat destruction and human persecution (Ripple et al. 2014; Treves and Bruskotter 2014). Where they co-occur, these species may be potentially competitors (de la Torre et al. 2016). However, the coexistence between these two felids may be facilitated by differential habitat and prey use, active avoidance, temporal or spatial segregation (Emmons 1987; Scognamillo et al. 2003; Azevedo 2008; Harmsen et al. 2009; Foster et al. 2010, 2013; Romero-Muñoz et al. 2010; Sollmann et al. 2012).

There is a wide variation in home-range sizes and body weight of jaguars and pumas in the Neotropics accordingly to the biome (Rabinowitz and Nottingham 1986; Iriarte et al. 1990; Crawshaw et al. 2004; Azevedo and Murray 2007; Cavalcanti and Gese 2009; Azevedo 2018; Ramalho and Magnusson 2018). Jaguars in the Pantanal of Brazil and Los Llanos in Venezuela are almost two times heavier than jaguars in the Atlantic Forest (Crawshaw and Quigley 1991; Crawshaw 1995; Scognamillo et al. 2003); the same relation applies to pumas from North and South America (Iriarte et al. 1990). Body weight is also correlated with spatial ecology and influence home range sizes, since species with heavier individuals usually have larger home ranges (Harestad and Bunnell 1979; Lindstedt et al. 1986; Morato et al. 2016). Habitat quality is another relevant factor that affects home range sizes. Jaguar and pumas may demand larger home ranges (Dickson and Beier 2002; Morato et al. 2016) to meet their resource needs depending on the quality of their habitats (Dickson and Beier 2002; Gehrt et al. 2009; Morato et al. 2016). In addition, individuals living in human-disturbed landscapes may be negatively affected by anthropic factors and demand larger home ranges (Azevedo 2018). In modified habitats, these species tend to vary their use of habitats by avoiding humans during the day and finding temporal refuges at night (Dickson and Beier 2002; Dickson et al. 2005; (Onorato et al. 2011 Lewis et al. 2015).

Comprehensive studies related to the spatial ecology of wild felids are still scarce in most of their distribution (Cullen Junior et al. 2013; de la Torre et al. 2016), especially in the Neotropics (Cavalcanti and Gese 2009; Laundré, J.W., Hernández 2010). Originally covering 1.395,848 km², currently only 163,774 km² (11.73%) of Atlantic Forest remains, distributed mostly in small fragments (< 1 km² that are isolated from each other) (Silva et al. 2007; Ribeiro et al. 2009). Only punctual spatial ecology studies were developed in this biome, since jaguar and puma populations have been locally

extinguished in the greatest portion of the Atlantic Forest (Cullen 2006; Paviolo et al. 2008, 2009; Beisiegel et al. 2012) and few patches of forest remain where both species persist simultaneously (Leite et al. 2002).

The present study sought to understand the spatial ecology of jaguars and pumas in the Rio Doce State Park - RDSP. We used GPS-collars to estimate home range sizes and the overlap between home ranges. In addition, we evaluated jaguar and puma habitat use and selection, accordingly to daytime (night and day). Given that these species are smaller and lighter in the Atlantic Forest, we expected the establishment of small home ranges in comparison to other areas where these cats occur and are larger and heavier. Secondly, as the RDSP is an isolated and small patch of Atlantic Forest surrounded by a matrix of altered habitats with intense human activity, we expected to find a high overlap between all monitored individuals. Finally, to avoid human modified habitats, we expected that both species would select natural instead of human-modified habitats. The use of human-modified habitats would occur predominantly at night hours.

MATERIALS AND METHODS

Ethics statement

Capture and handling of jaguars and pumas were approved by the ethics committee on the use of animals of the Federal University of São João del Rei - CEUA/UFSJ. The research project was authorized by the competent local authority ICMBio/SISBIO, under research permits 93896765/2015-2016 and 54311277/2016-2017.

Study area

The Rio Doce State Park - RDSP is an Atlantic Forest protected area in the state of Minas Gerais, southeastern Brazil (19°29' - 19°48' S / 42°28' - 42°38' W), covering

35,976 hectares (approximately 360 km²; Figure 1). It is one of the largest continuous extension of Atlantic Forest in Brazil and the largest in the Minas Gerais state (Gontijo and Britto 1997). The Rio Doce State Park still holds populations of endangered and vulnerable carnivores species such as the jaguar, the puma, and the jaguarundi (*Puma yagouarundi*) (Machado 1998; Pitman et al. 2002; IUCN 2016; Antonio De La Torre et al. 2018). Considering the degree of fragmentation of the Atlantic Forest, RDSP represents an important area for the maintenance of biodiversity in this environment (Silva Júnior et al. 2009). The vegetation is classified as “Submontane seasonal semideciduous forest” (IBGE 2012). The regional climate is classified as “humid subtropical”. Water is a abundant resource in the RDSP, since there are about 50 lakes inside the protected area (6% of its area), the northwest boundary is naturally set by the Piracicaba River and the Doce river to the east (IEF 1994) (Figure 1). Our study used a previously published detailed classification of land cover in the RDSP plus a 10 km buffer surrounding the park (Oliveira et al. 2019) (Figure 2). The buffer area is characterized by a wide diversity of socio-economic activities, such as agriculture, cattle ranching, mining and steel industries, which gives the region the name of “the steel valley” (Veloso et al. 1991) with some urbanized patches, with a dense human population (Oliveira et al. 2019). New activities have recently emerged in the region, such as a pulp industry encouraging the implementation of extensive monocultures of eucalyptus (*Eucalyptus* spp.) and sugar cane (*Saccharum officinarum*) (Oliveira et al. 2019) .

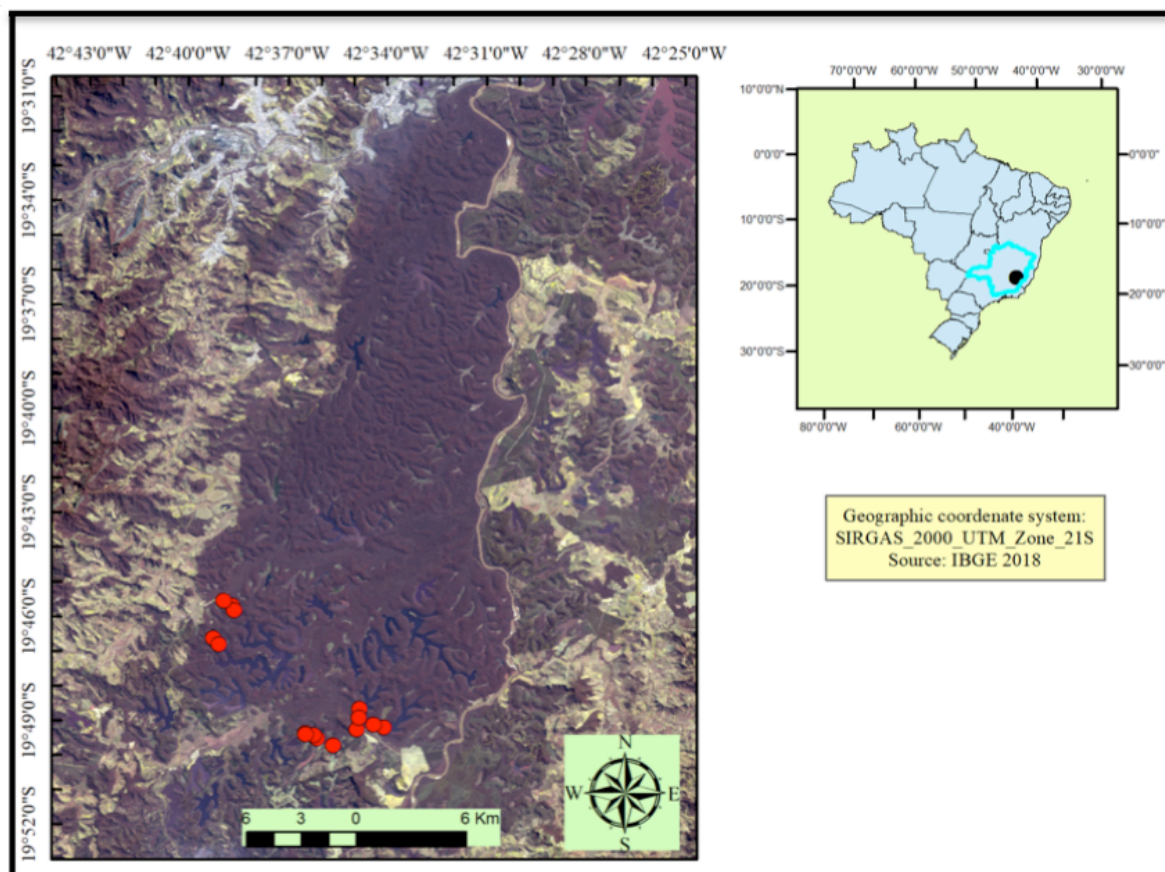


Figure 1. Map of the Rio Doce State Park and surroundings, red dots indicate the location of foot snares used to capture jaguars and pumas

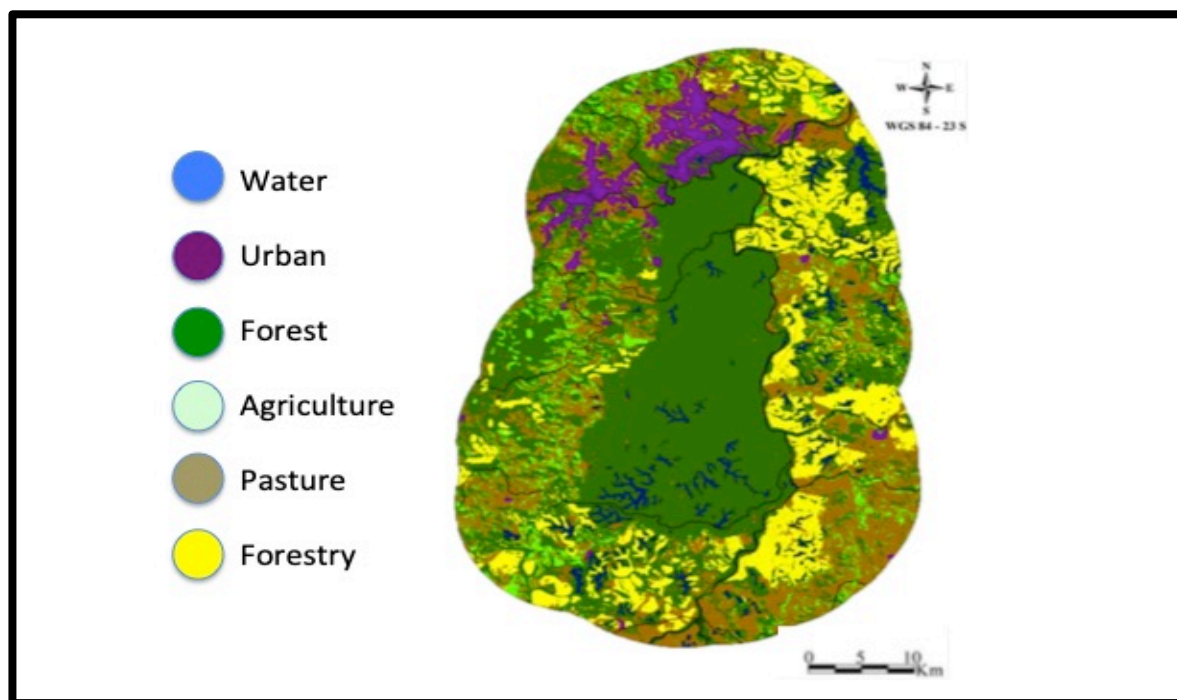


Figure 2. Land uses classes of the PERD buffer zone by classification of the LANDSAT-5/7/8 D.

Capture, handling and GPS telemetry data

We captured jaguars and pumas using foot snares (Logan et al. 1999; Frank et al. 2003; Elbroch et al. 2013) set in trails and dirt roads in the southern sector of RDSP (Figure 1). To minimize the risk of injury, we monitored traps by distance every two hours, using VHF-trap-transmitters (Trap-Transmitter/Nortronic, Brazil) (Halstead et al. 1995) and visually inspected at least once a day. We used an association of tiletamine-zolazepam at 10 mg/kg (Zoletil®, 100 mg, Virbac, São Paulo, Brazil) and xylazine at 1 mg/kg (Xilazin, 10%, Syntec, São Paulo, Brazil) for chemical restraint, administered via anesthetic dart. Captured animals passed through a complete clinical evaluation performed by a veterinarian. Based on physical characteristics such as presence of milk, teeth conditions (Stander 1997; Laundré et al. 2000) and pelage spotting progression (Shaw et al. 2007), we classified pumas as adults and sub adults. Animals received a Global Position System GPS-collar (Lotek® Fish & Wildlife Monitoring, Canada / 44400S and 4550S models; Sirtrack® Wildlife Track Solutions, New Zealand /G5C 375B Pinnacle GPS Iridium model). GPS-collars were programmed to collect geographical coordinate, date, time, activity and GPS accuracy (HDOP) every 2 hours. After complete recovery, animals were released at the same place of the capture and monitored for as long as the batteries lasted. All GPS-collars were equipped with a “drop-off” system, which automatically detaches the device from the animal when the batteries are low.

Home range and overlap analysis

We performed the estimation of jaguars and pumas home range and home range overlap using the software R 3.3.1 (R 2011) and the package ctmweb 0.2.5 (Continuous-Time Movement Modeling Web App) (Dong et al. 2018). We used the Autocorrelated Kernel Density Estimator (AKDE) (Fleming et al. 2015), a new estimator

that considers the dependency of the locations, to estimate home ranges with a ninety-five per cent confidence interval. Outlier coordinates were manually removed using the “Filter Outlier” tool in ctmweb. We used a one-week period where all the GPS-collars stood in a fixed location to generate a series of locations to calibrate the error of all subjacent data. The home range stability was verified through interpretation of variograms, which indicate if the monitored individual had established a determined territory during data collection period. Then we tested which model better adjusted to the data acquired (Brownian Motion BM, Integrated Orstein-Uhlenbek IOU, and Orstein-Uhlenbek Foraging OUF), using maximum likelihood based on Akaike Information Criterion. If the data-collection schedule of the GPS-collar was altered during monitoring period, we used the “Optimal Weighting” tool in order to correct the data. Then we estimated AKDE home range contours with 95% confidence intervals and quantified the overlap index among jaguars and pumas.

Habitat assessment

In order to perform the analysis on land use, we used the classification obtained by Oliveira *et al.*, 2019, using LANDSAT images captured in July 2015 (INPE 2015, Earth Explorer 2015). They used the software ArcGis (ESRI 2013) to map the land use (Earth Explorer 2015; INPE 2015) and classified the habitat in RDSP plus a 10 km buffer surrounding the protected area considering the following classes: water, forest, urban, forestry, pasture and agriculture (Oliveira *et al.* 2019).

Habitat use and selection analysis

We overlaid the land cover map to the locations obtained of all monitored individuals for habitat use and selection analysis. In addition, to verify if the temporal

scale influenced habitat use, we tested separately the locations obtained during night hours (from 18:00 h to 5:59 h) and day hours (from 06:00 h to 17:59 h) (van Schaik and Griffiths 2006). We used the software Ecological Methodology (Krebs 1999) to perform all the habitat use and selection analysis. First, we performed a χ^2 goodness-of-fit test to check if monitored animals used their home ranges randomly. Then we used the Manly standardized resource selection index for constant resources in order to compare locations obtained during the day and night hours among different habitat types. A Bonferroni Z-statistic tests adjustment was used to calculate 95% confidence intervals. We also tested the null hypothesis of non-selective locations based on the use and selection of habitats in relation to what was expected in terms of availability. Two categories were considered significantly different when their confidence intervals did not overlap. The selection ratios “W” for each habitat used were calculated as:

$$W = \frac{\text{number of locations per habitat}}{\text{habitat proportion available}}$$

The index value “W” indicates habitat avoidance when < 1 , use according to availability when $= 1$, and indicates habitat selection when > 1 . This outcome allows a direct comparison between selection ratios within each habitat type.

RESULTS

We captured two jaguars (one male and one female) and five pumas (two males and three females), from July 2017 to February 2018, with an effort of 712 trap-nights (6.91 in average, for 115 days), We also recaptured two pumas (one male and one female) and the female jaguar. Mean monitoring period of individuals was 405 days (± 200.8), totalizing 17,929 GPS locations (Table 1, Figure 3). All monitored individuals, except male puma 2, were considered residents after variogram evaluation (Figure 4),

confirming the reliability of the GPS data obtained to perform home range analysis. Therefore, we estimated home range and overlap using AKDE, using the OUF anisotropic model, model that best fitted for all monitored individuals (Table 2).

Table 1. Period of data collection, duration (days) and number of locations of all monitored individuals

Identity	Start	End	Duration	Locations
<i>Panthera onca</i> Female 1	9/23/17 23:26	7/8/18 21:01	288	2401
<i>Panthera onca</i> Male 1	11/7/17 22:40	12/18/18 23:00	405	2247
<i>Puma concolor</i> Female 1	7/28/17 0:06	5/1/19 22:11	624	4017
<i>Puma concolor</i> Female 2	9/8/17 2:29	4/16/18 19:00	219	1912
<i>Puma concolor</i> Female 3	9/15/17 0:40	5/20/19 11:01	613	4186
<i>Puma concolor</i> Male 1	7/28/17 8:40	9/8/18 16:13	409	3037
<i>Puma concolor</i> Male 2	12/7/17 13:23	12/21/17 21:00	15	129

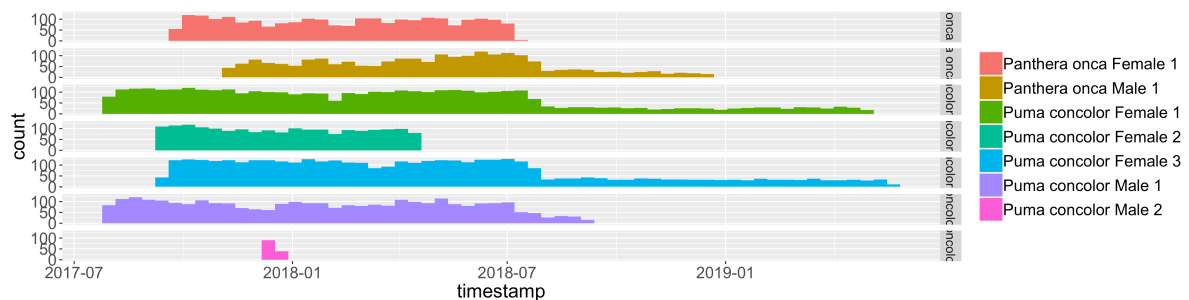


Figure 3. Data collection period of all monitored individuals

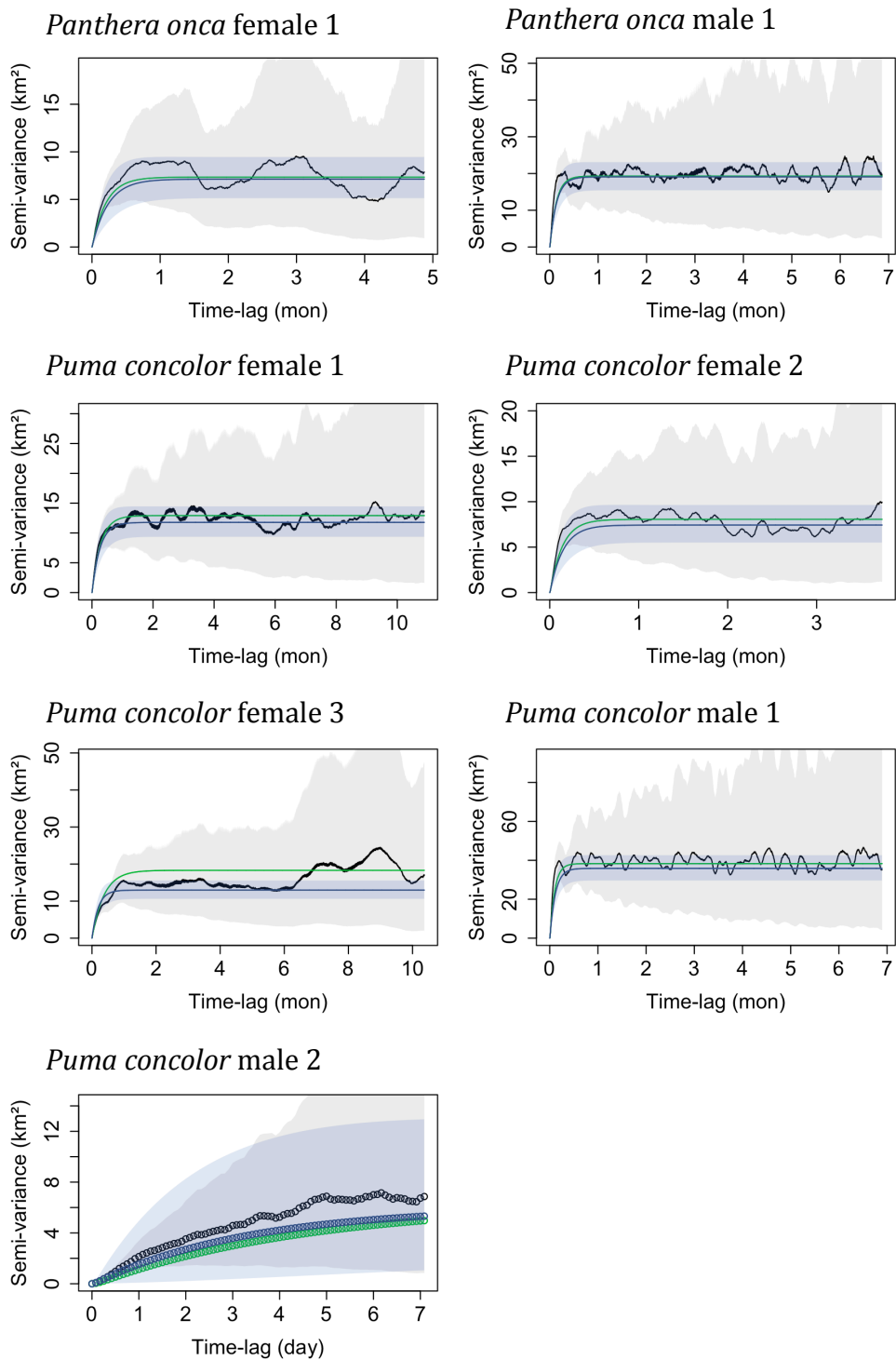


Figure 4. Variograms (semi-variance versus time-lag) of all monitored individuals, with model adjustment (blue line) and confidence intervals (blue envelope).

Table 2. Best-fitted model, home range estimated area and confidence intervals (95%) of all monitored individuals.

Identity	Model type	Area (km ²)	Area CI (km ²)
<i>Panthera onca</i> Female 1	OUF anisotropic	128.71	(92.66 – 170.6)
<i>Panthera onca</i> Male 1	OUF anisotropic	262.61	(212.4 – 318.06)
<i>Puma concolor</i> Female 1	OUF anisotropic	187.33	(149.01 – 229.97)
<i>Puma concolor</i> Female 2	OUF anisotropic	129.96	(96.29 – 168.62)
<i>Puma concolor</i> Female 3	OUF anisotropic	173.98	(142.34 – 208.75)
<i>Puma concolor</i> Male 1	OUF anisotropic	474.11	(391.75 – 564.22)
<i>Puma concolor</i> Male 2	OUF anisotropic	115.93	(36.35 – 240.83)

The estimated average area for jaguar home range (AKDE 95%) was 195.66 km² (95% CI: 152.53 – 244.33, n = 2); while for pumas it was 216.262 km² (95% CI: 163.14 – 282.47, n = 4) (Table 2, Figure 5). Since all individuals were monitored simultaneously, it was possible to estimate overlap among all of them (Figure 5). The overlap index varied from 0.17 (0.12 – 0.25 – *Panthera onca* female 1 and *Puma concolor* female 3) to 0.89 (0.70 – 0.96 – *Puma concolor* female 1 and *Puma concolor* female 2) (Figure 4, 5).

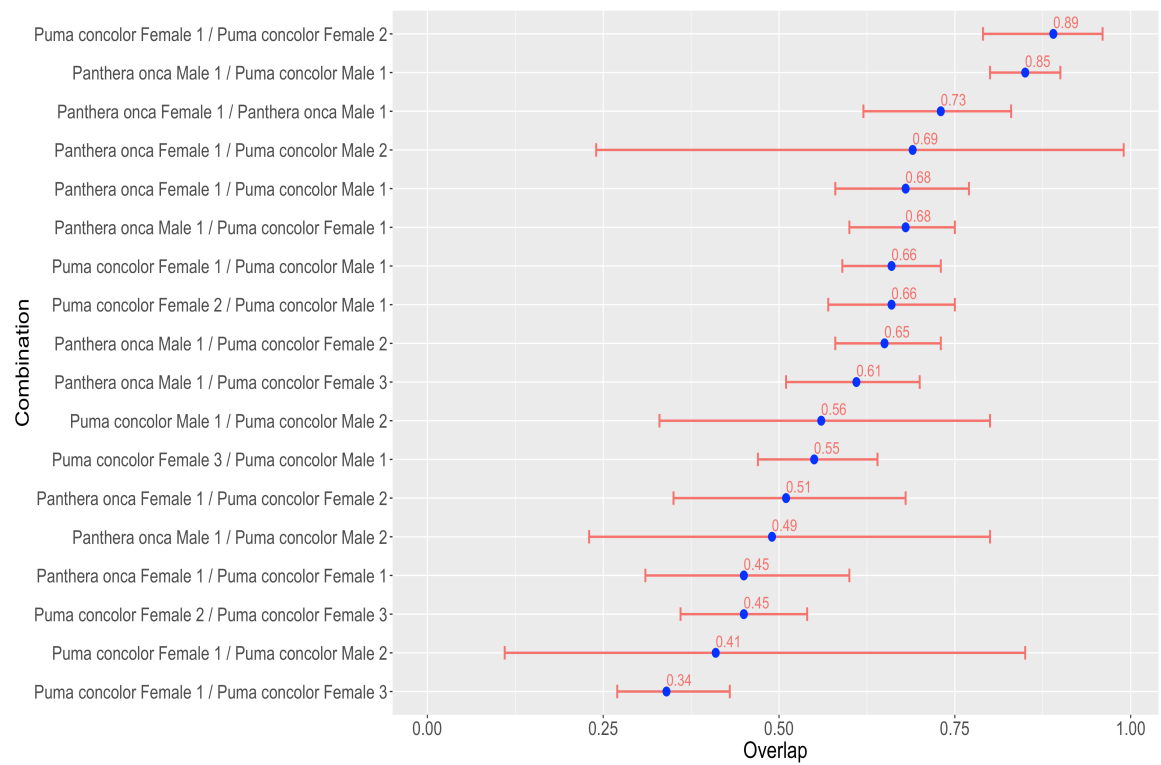


Figure 5. Overlap indexes obtained using 95% AKDE estimates (static interaction) between all monitored individuals

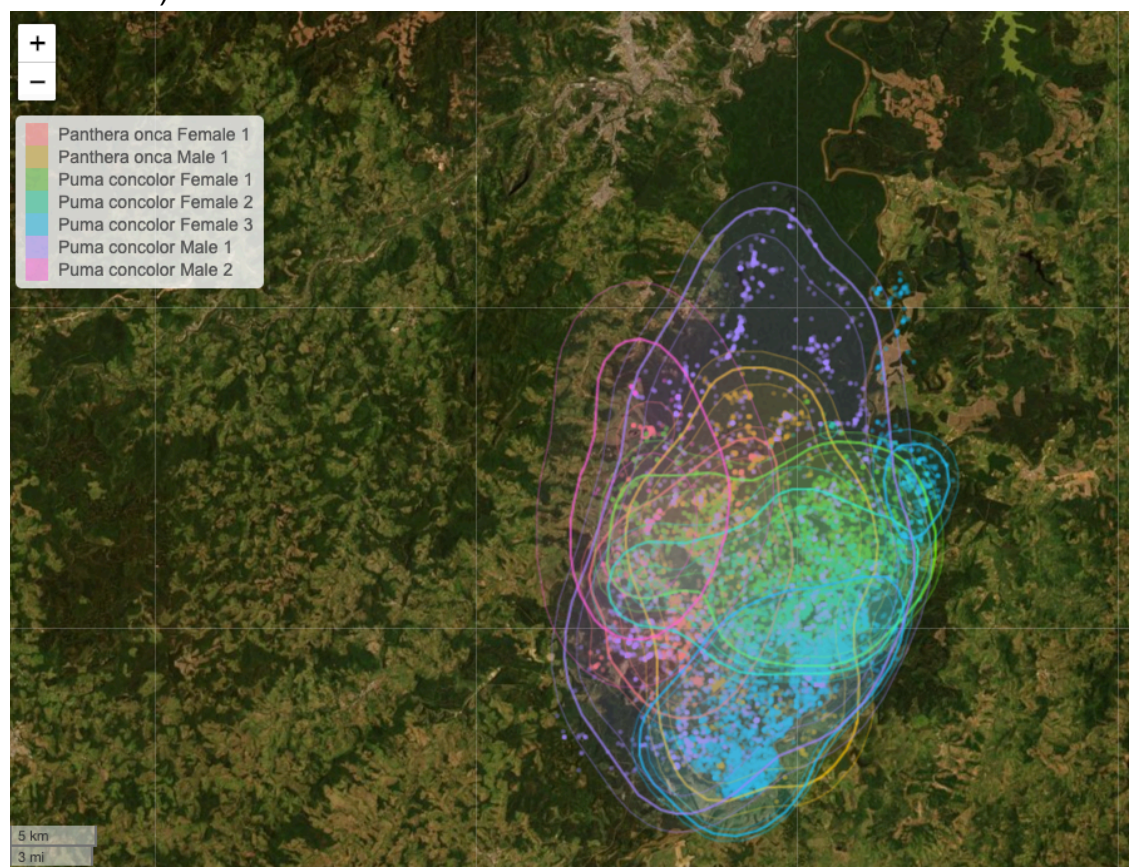


Figure 6. Overlap between home ranges (95% autocorrelated kernel density estimator - AKDE) of all individuals in RDPS, Minas Gerais, Brazil.

Both jaguars and pumas showed selection for determined habitats (Tables 3 and 4 respectively). Jaguars and pumas preferred forest and avoided urban areas, agriculture and pasture, independently of the daytime. The male jaguar also preferred water during the day and night, while females avoided it. The female jaguar showed preference for forestry during the night (Table 3). As for pumas, males avoided water during the day, but preferred during night hours, while females avoided water during night and day hours. As for forestry, puma males used as available during the day, but avoided during the night, while females preferred forestry during the day and used as available during the night (Table 4).

Table 3. Proportion of habitats used and habitat selection index (w) using Bonferroni Z-statistic tests with 95% confidence intervals for jaguars.

Sex	Period	Habitat	SPU	SPU - LI	SPU - UI	W	W-LI	W-UI	Selection		
						Standard					
Male	Day	Water	0.0689	0.0479	0.0899	0.1792	1.0811	2.027	Preferred		
		Urban	0	0	0	0	0	0	Avoided		
		Forest	0.8563	0.8273	0.8853	0.0227	1.7066	1.8265	Preferred		
		Agriculture	0.003	0	0.0074	0.0274	0	0.1199	Avoided		
		Pasture	0.0187	0.0075	0.0299	0.0188	0.033	0.132	Avoided		
		Forestry	0.0531	0.0346	0.0717	0.05	0.2454	0.5091	Avoided		
	Night										
		Water	0.0704	0.0508	0.0899	0.1669	1.1459	2.0266	Preferred		
		Urban	0	0	0	0	0	0	Avoided		
		Forest	0.8384	0.8102	0.8665	0.022	1.6723	1.7883	Preferred		
		Agriculture	0.0042	0	0.0091	0.0302	0	0.1473	Avoided		
		Pasture	0.036	0.0218	0.0502	0.0238	0.0961	0.2215	Avoided		
Forestry	0.0511	0.0343	0.0679	0.0451	0.2424	0.4801	Avoided				

		Water	Urban	Forest	Agriculture	Pasture	Forestry		
Female	Day	Water	0.0439	0.0277	0.0601	0.1397	0.6314	1.3686	Preferred
		Urban	0	0	0	0	0	0	Avoided
		Forest	0.8665	0.8396	0.8934	0.021	1.732	1.8429	Preferred
		Agriculture	0.0027	0	0.0068	0.0251	0	0.1096	Avoided
		Pasture	0.0305	0.0169	0.044	0.0227	0.0745	0.1943	Avoided
		Forestry	0.0565	0.0382	0.0747	0.0488	0.27	0.5275	Avoided
	Night	Water	0.009	0.0056	0.0124	0.0292	0.1263	0.2805	Avoided
		Urban	0	0	0	0	0	0	Avoided
		Forest	0.7377	0.7218	0.7536	0.0124	1.4895	1.5551	Preferred
		Agriculture	0.0015	0.0001	0.0029	0.0086	0.0016	0.0468	Avoided
		Pasture	0.0905	0.0801	0.1009	0.0173	0.3536	0.4451	Avoided
		Forestry	0.1613	0.148	0.1746	0.0357	1.0481	1.2365	Preferred

SPU = sample proportion used, W = selection ratios, calculated as the number of locations per habitat divided by the habitat proportion available, LI = lower confidence interval, UI = upper confidence interval.

Table 4. Proportion of habitats used and habitat selection index (w) using Bonferroni Z-statistic tests with 95% confidence intervals for pumas.

Sex	Period	Habitat	SPU	SPU - LI	SPU - UI	W			Selection
						Standard	W-LI	W-UI	
Male	Day	Water	0.0212	0.0165	0.0259	0.0405	0.3721	0.5858	Avoided
		Urban	0	0	0	0	0	0	Avoided
		Forest	0.7655	0.7516	0.7794	0.0109	1.5507	1.608	Preferred
		Agriculture	0.0029	0.0012	0.0047	0.0109	0.0187	0.076	Avoided
		Pasture	0.0668	0.0586	0.075	0.0137	0.2585	0.3308	Avoided
		Forestry	0.1436	0.1321	0.1551	0.0309	0.9359	1.0989	Used as Available
	Night	Water	0.0704	0.0544	0.0863	0.137	1.2334	1.9564	Preferred
		Urban	0.0006	0	0.002	0.0135	0	0.0492	Avoided
		Forest	0.7728	0.7466	0.7989	0.0204	1.5406	1.6484	Preferred
		Agriculture	0.0084	0.0027	0.0141	0.0347	0.0435	0.2268	Avoided
		Pasture	0.0581	0.0435	0.0727	0.0244	0.1918	0.3205	Avoided
		Forestry	0.0899	0.0721	0.1077	0.0478	0.5101	0.7626	Avoided

Female	Day	Water	0.0119	0.0078	0.0161	0.0354	0.1755	0.3623	Avoided
		Urban	0	0	0	0	0	0	Avoided
		Forest	0.7548	0.7384	0.7712	0.0128	1.5233	1.5911	Preferred
		Agriculture	0.0008	0	0.0019	0.0068	0	0.0313	Avoided
		Pasture	0.0745	0.0645	0.0846	0.0168	0.2848	0.3733	Avoided
		Forestry	0.1579	0.144	0.1718	0.0374	1.02	1.2173	Preferred
	Night	Water	0.009	0.0056	0.0124	0.0276	0.1192	0.2647	Avoided
		Urban	0	0	0	0	0	0	Avoided
		Forest	0.7377	0.7218	0.7536	0.0133	1.5904	1.6605	Preferred
		Agriculture	0.0015	0.0001	0.0029	0.0081	0.0016	0.0442	Avoided
		Pasture	0.0905	0.0801	0.1009	0.0164	0.3336	0.42	Avoided
		Forestry	0.1613	0.148	0.1746	0.0337	0.9891	1.1668	Used as Available

SPU = sample proportion used, W = selection ratios, calculated as the number of locations per habitat divided by the habitat proportion available, LI = lower confidence interval, UI = upper confidence interval.

Discussion

The home range sizes we obtained for jaguars and pumas were larger compared to sizes in other environments (Gonzalez-Borrajo et al. 2017), using different estimators (MCP and KDE). This difference was expected, since home range estimates using AKDE are usually larger than those using KDE estimates (based on the same data). Jaguars and pumas in RDSP showed either smaller and bigger home ranges than in other environments, therefore we did not confirm or refute our initial hypothesis about the proportion of body weight and home range size. Both species showed smaller home-ranges when compared to other studies in the Atlantic Forest, nevertheless, these studies used small sample sizes (Paula et al., 2015; Morato et al., 2016) indicating caution in this comparison. In addition, the lighter weight of both species in the Atlantic Forest compared to other biomes, may have influenced the establishment of smaller home ranges as reported elsewhere (Harestad and Bunnell 1979; Lindstedt et al. 1986). Small home ranges may also be an indication of good environmental quality, since home ranges are predicted to decrease with good habitat quality (Dickson and Beier 2002; Fahrig 2007; Morato et al. 2016). In some ecosystems, home range size may be inversely related to density of carnivores and prey availability (Davies and Houston 1984; Dahle and Swenson 2003).

We found high intra and interspecific overlap among all individuals, which confirms our initial hypothesis. This high overlap between home ranges may indicate that food resource may vary in space and time, since exclusive ranges are expected when food resources are stable and evenly distributed, whereas overlapping ranges is likely when the timing and spacing of available prey varies (Sandell 1989), which may be the case in RDSP. The small number of monitored individuals in our study limited the assessment of male–female spatial overlap for both species. Nonetheless, as expected

for territorial carnivores, both jaguar and puma males overlapped significantly with females (Logan and Sweanor 2001; Azevedo and Murray 2007; Macdonald and Loveridge 2010). A single male may encompass the territory of several females (Logan and Sweanor 2010; Elbroch and Wittmer 2012; Elbroch and Quigley 2017). This situation was similar to what we found in our study, where all monitored female pumas showed high intra sexual overlap and a high overlap with male puma 1. Male 1 had the largest territory in RDSP, almost totally encompassing female home ranges.

While most studies of co-existence between jaguars and pumas investigated differences in their diet, our results showed that jaguars and pumas were present and used the available habitat with a similar intensity, supporting the theory that the partitioning of food resources between both species could be influenced by their partitioning of space and by habitat preferences of prey species of common interest (Foster et al. 2010; Sollmann et al. 2012). Jaguars and pumas preferred natural habitats, such as forest and water. However, our hypothesis that both species would select native instead of human-modified habitats was confirmed for urban areas and agriculture, but not for forestry. Female jaguars preferred forestry during the night and female pumas preferred it during the day. Both male and female pumas used forestry as available during the night hours. The use of forestry by pumas and jaguars may be related to facilitation of movement across the landscape. To access natural forest areas outside the RDSP (in the 10 km buffer zone), these animals must move through a matrix of forestry and other plantations. Moreover, the use of anthropic areas may be a way of optimizing predation opportunities (Miotto et al. 2012; Magioli et al. 2014), because these areas are also used by prey species that require a mix of open and close canopy habitats (e.g. brocket deer *Mazama gouazoubira*, and capybara *Hydrochaeris hydrochaeris*; Azevedo 2018).

Our data showed that the use of human-modified habitats predominantly during night hours occurred only for the female jaguar, which preferred forestry during night hours, and for the female pumas, which used forestry as available during the night. For the jaguar and puma females in our study, the use of modified habitats during night hours may also be related to avoidance of contact with males (Cavalcanti and Gese 2009; Azevedo 2018), since the female jaguar and female pumas preferred forestry in periods that males avoided it or used as available. In addition, carnivores living close to urban areas may avoid human disturbances during the day and find temporal refuge from human activities at night (Lewis et al. 2015). Both jaguar and puma males preferred water during night hours, when the capybara, a key prey species of jaguars and pumas in the Atlantic Forest (Azevedo et al. 2018; Franco et al. 2018), is feeding by the water. These findings do not necessarily mean that jaguar and puma females do not prey capybaras, since it may be also a reflection of male avoidance in this habitat during this period of the day. In addition, jaguar and puma females may prey capybaras in other habitats, such as forest, which both species preferred, for example.

Despite of the highest effort reported to capture large sized felids in the Atlantic forest, our capture success was low and similar to what has been previously reported for this environment (Araujo 2016). Although our sample size was small, this is the first study to collect spatial data of jaguars and pumas simultaneously in the Atlantic Forest. The long data collection period, the precision of GPS-collar technology and the innovations of the AKDE analysis, allowed us to estimate accurately home range and overlap (Hebblewhite and Haydon 2010). The AKDE is a recent analytical improvement in spatial ecology, capable of removing negative bias in home range estimation by incorporating the autocorrelation structure inherent in most movement datasets (Fleming et al. 2015; Calabrese et al. 2016). Therefore, we believe that our home ranges

estimates reliably reflected individual's behavior, since the variogram analysis indicated range stability, as individuals territories semi-variance reached an asymptote (Fleming et al. 2015; Morato et al. 2016) (Figure 3). The only exception was male puma 2, which had a short data collection period, making impossible to accurately estimate its home range.

Conclusion and Recommendations

Our study provides novel and modern information on the spatial ecology and use of the landscape by jaguars and pumas in the Atlantic Forest, contributing to the long-term conservation and management of large carnivores in this environment. Our results emphasize the importance of maintaining large natural areas for jaguars and pumas in the Atlantic Forest, since these species occur in low densities and have large home ranges; large areas are necessary to maintain long-term population viability (genetically and demographically). To improve our understanding of the predator-prey relationship and its consequences on the spatial ecology of jaguars and pumas in the RDSP and surroundings, a higher number of monitored jaguars and pumas are necessary. Moreover, more efforts focusing on investigating prey densities and distribution, predator and prey population dynamics and large-sized felids diet are necessary. It is essential that viable territories for jaguars and pumas must be restored and protected around the RDSP within private areas (e.g. legal reserves and environmental protection areas, as predicted by law in Brazil), thus increasing chances of maintenance and survival of their populations in this portion of the Atlantic Forest.

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Supplementary Material

Table S1. Overlap indexes obtained using 95% AKDE estimates (static interaction) between all monitored individuals

v1	v2	Index	CI low	CI high
<i>Panthera onca</i> Female 1	<i>Panthera onca</i> Male 1	0.73	0.62	0.83
<i>Panthera onca</i> Female 1	<i>Puma concolor</i> Female 1	0.45	0.31	0.6
<i>Panthera onca</i> Female 1	<i>Puma concolor</i> Female 2	0.51	0.35	0.68
<i>Panthera onca</i> Female 1	<i>Puma concolor</i> Female 3	0.17	0.12	0.25
<i>Panthera onca</i> Female 1	<i>Puma concolor</i> Male 1	0.68	0.58	0.77
<i>Panthera onca</i> Female 1	<i>Puma concolor</i> Male 2	0.69	0.24	0.99
<i>Panthera onca</i> Male 1	<i>Puma concolor</i> Female 1	0.68	0.6	0.75
<i>Panthera onca</i> Male 1	<i>Puma concolor</i> Female 2	0.65	0.58	0.73
<i>Panthera onca</i> Male 1	<i>Puma concolor</i> Female 3	0.61	0.51	0.7
<i>Panthera onca</i> Male 1	<i>Puma concolor</i> Male 1	0.85	0.8	0.9
<i>Panthera onca</i> Male 1	<i>Puma concolor</i> Male 2	0.49	0.23	0.8
<i>Puma concolor</i> Female 1	<i>Puma concolor</i> Female 2	0.89	0.79	0.96
<i>Puma concolor</i> Female 1	<i>Puma concolor</i> Female 3	0.34	0.27	0.43
<i>Puma concolor</i> Female 1	<i>Puma concolor</i> Male 1	0.66	0.59	0.73
<i>Puma concolor</i> Female 1	<i>Puma concolor</i> Male 2	0.41	0.11	0.85
<i>Puma concolor</i> Female 2	<i>Puma concolor</i> Female 3	0.45	0.36	0.54
<i>Puma concolor</i> Female 2	<i>Puma concolor</i> Male 1	0.66	0.57	0.75
<i>Puma concolor</i> Female 2	<i>Puma concolor</i> Male 2	0.28	0.05	0.76
<i>Puma concolor</i> Female 3	<i>Puma concolor</i> Male 1	0.55	0.47	0.64
<i>Puma concolor</i> Female 3	<i>Puma concolor</i> Male 2	0.01	0	0.05
<i>Puma concolor</i> Male 1	<i>Puma concolor</i> Male 2	0.56	0.33	0.8

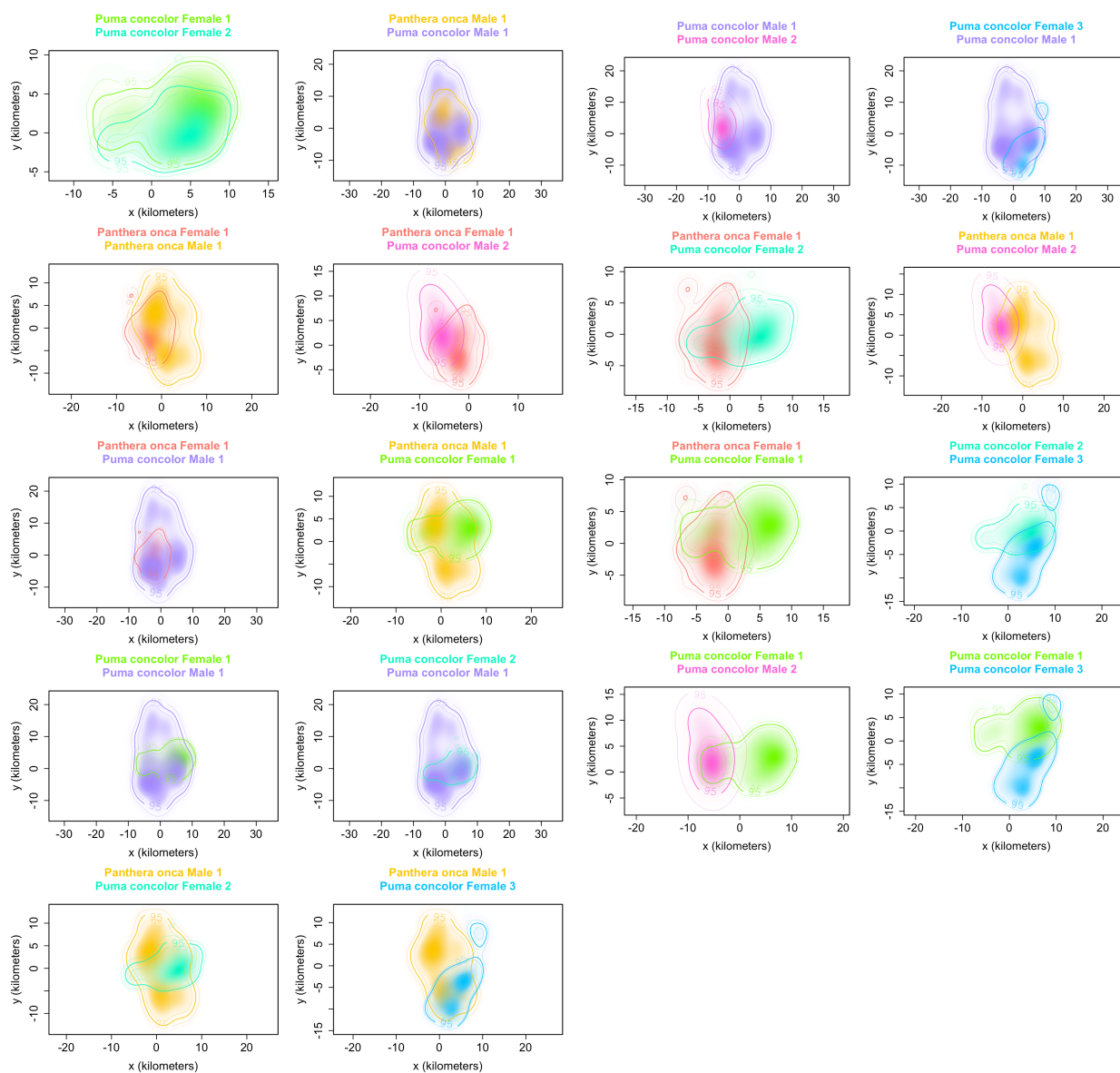


Figure S1. Overlap between home ranges of paired individuals using the 95% Auto correlated Kernel Density Estimator (AKDE) in RDPS, Minas Gerais, Brazil.

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AUTORIZAÇÕES PARA ATIVIDADES COM FINALIDADE CIENTÍFICA

2015-2016



Ministério do Meio Ambiente - MMA
 Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio
 Sistema de Autorização e Informação em Biodiversidade - SISBIO

Autorização para atividades com finalidade científica

Número: 34284-3	Data da Emissão: 25/05/2015 06:25	Data para Revalidação*: 23/06/2016
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* De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.

Dados do titular

Nome: FERNANDO CESAR CASCELLI DE AZEVEDO	CPF: 552.582.201-68
Título do Projeto: AVALIAÇÃO DA PREDACÃO DE ONÇAS SOBRE ANIMAIS DOMÉSTICOS E PERFIL SANITÁRIO DE CARNÍVOROS SILVESTRES NA REGIÃO DO PARQUE ESTADUAL DO RIO DOCE, MINAS GERAIS	
Nome da Instituição : UNIVERSIDADE FEDERAL DE SÃO JOÃO DEL REI	CNPJ: 21.186.804/0001-05

Cronograma de atividades

#	Descrição da atividade	Início (mês/ano)	Fim (mês/ano)
1	Visitas às propriedades do entorno	07/2012	10/2012
2	Instalação e checagem de armadilhas fotográficas e monitoramento de animais capturados	01/2013	12/2016
3	Análise dos resultados obtidos	01/2014	06/2016
4	Visitas às propriedades e realização das entrevistas	07/2015	12/2015
5	Captura de carnívoros silvestres	08/2015	12/2016
6	Análise dos dados coletados durante as entrevistas	12/2015	04/2016

Observações e ressalvas

1	As atividades de campo exercidas por pessoa natural ou jurídica estrangeira, em todo o território nacional, que impliquem o deslocamento de recursos humanos e materiais, tendo por objeto coletar dados, materiais, espécimes biológicos e minerais, peças integrantes da cultura nativa e cultura popular, presente e passada, obtidos por meio de recursos e técnicas que se destinem ao estudo, à difusão ou à pesquisa, estão sujeitas a autorização do Ministério de Ciência e Tecnologia.
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Equipe

#	Nome	Função	CPF	Doc. Identidade	Nacionalidade
1	Cynthia Elisa Widmer	Médica Veterinária	041.623.329-59	435072328 SSP-SP	Brasileira
2	RICARDO LUIZ PIRES BOULHOSA	Assistente de campo	253.726.018-09	122555119 SSP-SP	Brasileira

Locais onde as atividades de campo serão executadas

#	Município	UF	Descrição do local	Tipo
1	DIONÍSIO	MG	Parque Estadual do Rio Doce	Fora de UC Federal
2	MARLIERIA	MG	Parque Estadual do Rio Doce	Fora de UC Federal

Este documento (Autorização para atividades com finalidade científica) foi expedido com base na Instrução Normativa nº 03/2014. Através do código de autenticação abaixo, qualquer cidadão poderá verificar a autenticidade ou regularidade deste documento, por meio da página do Sisbio/ICMBio na Internet (www.icmbio.gov.br/sisbio).

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2016-2017



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Autorização para atividades com finalidade científica

Número: 34284-4	Data da Emissão: 20/01/2016 16:35	Data para Revalidação*: 18/02/2017
* De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.		

Dados do titular

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Título do Projeto: AVALIAÇÃO DA PREDACÃO DE ONÇAS SOBRE ANIMAIS DOMÉSTICOS E PERFIL SANITÁRIO DE CARNÍVOROS SILVESTRES NA REGIÃO DO PARQUE ESTADUAL DO RIO DOCE, MINAS GERAIS	
Nome da Instituição : UNIVERSIDADE FEDERAL DE SÃO JOÃO DEL REI	CNPJ: 21.186.804/0001-05

Cronograma de atividades

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Observações e ressalvas

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5	O titular de licença ou autorização e os membros da sua equipe deverão optar por métodos de coleta e instrumentos de captura direcionados, sempre que possível, ao grupo taxonômico de interesse, evitando a morte ou dano significativo a outros grupos; e empregar esforço de coleta ou captura que não comprometa a viabilidade de populações do grupo taxonômico de interesse em condição in situ.
6	O titular de autorização ou de licença permanente, assim como os membros de sua equipe, quando da violação da legislação vigente, ou quando da inadequação, omissão ou falsa descrição de informações relevantes que subsidiaram a expedição do ato, poderá, mediante decisão motivada, ter a autorização ou licença suspensa ou revogada pelo ICMBio, nos termos da legislação brasileira em vigor.
7	Este documento não dispensa o cumprimento da legislação que dispõe sobre acesso a componente do patrimônio genético existente no território nacional, na plataforma continental e na zona econômica exclusiva, ou ao conhecimento tradicional associado ao patrimônio genético, para fins de pesquisa científica, bioprospecção e desenvolvimento tecnológico. Veja maiores informações em www.mma.gov.br/cgen.
8	Em caso de pesquisa em UNIDADE DE CONSERVAÇÃO, o pesquisador titular desta autorização deverá contactar a administração da unidade a fim de CONFIRMAR AS DATAS das expedições, as condições para realização das coletas e de uso da infra-estrutura da unidade.

Equipe

#	Nome	Função	CPF	Doc. Identidade	Nacionalidade
1	Cynthia Elisa Widmer	Médica Veterinária	041.623.329-59	435072328 SSP-SP	Brasileira
2	RICARDO LUIZ PIRES BOULHOSA	Assistente de campo	253.726.018-09	122555119 SSP-SP	Brasileira

Locais onde as atividades de campo serão executadas

#	Município	UF	Descrição do local	Tipo
1	DIONISIO	MG	Parque Estadual do Rio Doce	Fora de UC Federal
2	MARLIERIA	MG	Parque Estadual do Rio Doce	Fora de UC Federal

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Código de autenticação: 45311277



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2017-2018



Ministério do Meio Ambiente - MMA
 Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio
 Sistema de Autorização e Informação em Biodiversidade - SISBIO

Autorização para atividades com finalidade científica

Número: 34284-6	Data da Emissão: 02/02/2017 07:05	Data para Revalidação*: 04/03/2018
* De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.		

Dados do titular

Nome: FERNANDO CESAR CASCELLI DE AZEVEDO	CPF: 552.582.201-68
Título do Projeto: AVALIAÇÃO DA PREDACÃO DE ONÇAS SOBRE ANIMAIS DOMÉSTICOS E PERFIL SANITÁRIO DE CARNÍVOROS SILVESTRES NA REGIÃO DO PARQUE ESTADUAL DO RIO DOCE, MINAS GERAIS	
Nome da Instituição : UNIVERSIDADE FEDERAL DE SÃO JOÃO DEL REI	CNPJ: 21.186.804/0001-05

Cronograma de atividades

#	Descrição da atividade	Início (mês/ano)	Fim (mês/ano)
1	Visitas as propriedades do entorno	07/2012	10/2018
2	Instalação e checagem de armadilhas fotográficas e monitoramento de animais capturados	01/2013	12/2018
3	Análise dos resultados obtidos	01/2014	06/2018
4	Visitas as propriedades e realização das entrevistas	07/2015	12/2015
5	Captura de carnívoros silvestres	08/2015	12/2018
6	Análise dos dados coletados durante as entrevistas	12/2015	04/2018

Observações e ressalvas

1	As atividades de campo exercidas por pessoa natural ou jurídica estrangeira, em todo o território nacional, que impliquem o deslocamento de recursos humanos e materiais, tendo por objeto coletar dados, materiais, espécimes biológicos e minerais, peças integrantes da cultura nativa e cultura popular, presente e passada, obtidos por meio de recursos e técnicas que se destinem ao estudo, à difusão ou à pesquisa, estão sujeitas a autorização do Ministério de Ciência e Tecnologia.
2	Esta autorização NÃO exige o pesquisador titular e os membros de sua equipe da necessidade de obter as anuências previstas em outros instrumentos legais, bem como do consentimento do responsável pela área, pública ou privada, onde será realizada a atividade, inclusive do órgão gestor de terra indígena (FUNAI), da unidade de conservação estadual, distrital ou municipal, ou do proprietário, arrendatário, posseiro ou morador de área dentro dos limites de unidade de conservação federal cujo processo de regularização fundiária encontra-se em curso.
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Equipe

#	Nome	Função	CPF	Doc. Identidade	Nacionalidade
1	Cynthia Elisa Widmer	Médica Veterinária	041.623.329-59	435072328 SSP-SP	Brasileira
2	RICARDO LUIZ PIRES BOULHOSA	Assistente de campo	253.726.018-09	122555119 SSP-SP	Brasileira
3	RICARDO CORASSA ARRAISRI	Responsável pelas atividades de campo	311.495.088-41	284103603 SSP-SP	Brasileira

Locais onde as atividades de campo serão executadas

#	Município	UF	Descrição do local	Tipo
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Código de autenticação: 87259952



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2018-2019



Ministério do Meio Ambiente - MMA
 Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio
 Sistema de Autorização e Informação em Biodiversidade - SISBIO

Autorização para atividades com finalidade científica

Número: 34284-7	Data da Emissão: 13/02/2018 15:05	Data para Revalidação*: 15/03/2019
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* De acordo com o art. 28 da IN 03/2014, esta autorização tem prazo de validade equivalente ao previsto no cronograma de atividades do projeto, mas deverá ser revalidada anualmente mediante a apresentação do relatório de atividades a ser enviado por meio do Sisbio no prazo de até 30 dias a contar da data do aniversário de sua emissão.

Dados do titular

Nome: FERNANDO CESAR CASCELLI DE AZEVEDO	CPF: 552.582.201-68
Título do Projeto: AVALIAÇÃO DA PREDACÃO DE ONÇAS SOBRE ANIMAIS DOMÉSTICOS E PERFIL SANITÁRIO DE CARNÍVOROS SILVESTRES NA REGIÃO DO PARQUE ESTADUAL DO RIO DOCE, MINAS GERAIS	
Nome da Instituição : UNIVERSIDADE FEDERAL DE SÃO JOÃO DEL REI	CNPJ: 21.186.804/0001-05

Cronograma de atividades

#	Descrição da atividade	Início (mês/ano)	Fim (mês/ano)
1	Visitas as propriedades do entorno	07/2012	10/2018
2	Instalação e checagem de armadilhas fotográficas e monitoramento de animais capturados	01/2013	12/2018
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6	Análise dos dados coletados durante as entrevistas	12/2015	04/2018

Observações e ressalvas

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Locais onde as atividades de campo serão executadas

#	Município	UF	Descrição do local	Tipo
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PARECER DO COMITÊ DE ÉTICA

Comissão de Ética no Uso de Animais da UFSJ – CEUA/UFSJ

CERTIFICADO

Certificamos que o protocolo para uso de animais em experimentação nº 03/2013, sobre o projeto pesquisa: "Avaliação da Predação de Onças sobre Animais Domésticos e Perfil Sanitário de Carnívoros Silvestres na Região do parque Estadual do Rio Doce, Minas Gerais". sob a responsabilidade: Prof. Fernando Cesar Cascelli de Azevedo está de acordo com os Princípios Éticos na Experimentação Animal, dispostos na Lei Federal nº 11.794, de 08.10.2008, e foi aprovado pela Comissão de Ética no Uso de Animais - CEUA-UFSJ - em reunião no dia 22 março de 2013.

São João del-Rei, 26 de Março de 2013.

Prof. Dr. Gilcélio Amaral da Silveira
Coordenador da CEUA/UFSJ