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From large to small-scale: drivers of Geoffroy´s cat diet across South America and features of life-history in a human-modified landscape on southern Brazil

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From large to small-scale: drivers of Geoffroy´s cat diet change across South America and features of life-history to persist in human-modified landscape on southern Brazil

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Thesis presented as a requirement to obtain the Doctor's degree in Ecology and Conservation, by the Post Graduate Program in Ecology and Conservation, Federal University of Mato Grosso do Sul.

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General Abstract

1. Mammalian carnivores plays a crucial role in nature by providing top-down control of communities. Their ecological influences are mostly driven by the spatial features, intra- and inter-specific interactions. Understanding the predator-prey interaction and how carnivores deal with the landscape changes are central concerns in studies of this guild. Due to its wide geographical distribution and by inhabit distinct habitats, the Geoffroy´s cat *Leopardus geoffroyi* has become an excellent model to study this inconspicuous interaction.

2. In this study, we addressed two aspects of Geoffroy´s cat ecology. The first was in large scale, where we investigate how the diet structure changes in latitudinal, altitudinal and human disturbances gradient. The second was in small scale, we aimed to estimate the home ranges size, habitat selection and activity patterns of this small carnivore in an intensely human-modified landscape.

3. We reviewed 20 studies of Geoffroy´s cat diet across South America and measure the effects of drivers on diet structure, specialization and mean of mammal prey size. Besides, we tracked 14 Geoffroy´s cat by GPS collars on the Pampa ecoregion in south of Brazil to determine how it uses this space. We used a Structural Equation Modelling to test our hypothesized relations of diet changes in large scale. We estimated the home ranges sizes by minimum-convex-polygon and Kernel techniques and we estimated the habitat selection and activity patterns by Step Selection analysis.

4. *Cavia*, *Ctenomys* and *Lepus* are the Geoffroy´s cat main preys across South America. The latitude, human disturbances and especially altitude had direct and indirect effects on diet structure, specialization and prey size selection. In southern Brazil, human-modified landscape the Geoffroy´s home ranges size is as larger as the other regions of South America. Males are larger than females and the home range

increases with the male body size. Geoffroy´s cat selected forest both at night and day. Rice fields, water bodies and farmhouses were selected at nocturnal period and avoided at daylight. Pastures are always avoided.

5. All diet drivers have led to prey turnover along the biogeographical and anthropogenic gradients. Physical and biological landscapes constraints may explain these changes. Diet specialization was correlated with consumption of large prey, mainly *Lepus*. Our refined tracking data reinforces the predictions that Geoffroy´s cat is tolerant when subjected to human-modified habitats. The intense use of managed areas supports this statement. Riparian forest and water bodies habitats play an essential role to Geoffroy´s cat in human-modified landscape on southernmost Brazil.

Key-words: altitude, habitat selection, home range, latitude, *Leopardus geoffroyi*, Pampa biome

Resumo Geral

1. Os mamíferos carnívoros desempenham um papel crucial na natureza, exercendo controle ‘top-down’ nas comunidades. Sua influência ecológica é principalmente impulsionada pelas características espaciais e interações intra e interespecíficas. Compreender a relação predador-presa e como carnívoros lidam com as mudanças na paisagem são questões centrais nos estudos desta guilda. Por apresentar ampla distribuição geográfica e por habitar diferentes ambientes, o gato-do-mato *Leopardus geoffroyi* se tornou um excelente modelo para estudar essas relações.

2. Neste estudo foram abordados dois aspectos da ecologia do gato-do-mato. O primeiro em larga escala, onde investigamos como a estrutura da dieta muda no gradiente de latitude, altitude e distúrbios humanos. O segundo em pequena escala, com o objetivo de estimar o tamanho da área de vida, seleção de habitat e o padrão de atividade deste pequeno carnívoro em uma paisagem intensamente modificada pelo homem.

3. Nós revisamos 20 estudos de dieta do gato-do-mato em toda a América do Sul e medimos os efeitos dos impulsionadores de mudanças na estrutura da dieta, especialização e tamanho médio do mamífero presa. Além disso, rastreamos 14 gatos-do-mato utilizando colares GPS para determinar como os felinos usam o espaço em uma área no Bioma Pampa no sul do Brasil. Utilizamos Modelagem de Equações Estruturais para testar as hipóteses de relações de mudanças na dieta em larga escala. E estimamos os tamanhos das áreas de vida por meio das técnicas de mínimo polígono convexo e Kernel, além de determinar a seleção de habitat e o padrão de atividade por meio da análise de seleção de passos.

4. *Cavia*, *Ctenomys* e *Lepus* são as principais presas do gato-do-mato em toda a América do Sul. A latitude, distúrbios humanos e especialmente a altitude tiveram

efeitos diretos e indiretos na estrutura da dieta, especialização e seleção do tamanho de presas. No sul do Brasil, o tamanho das áreas de vida é tão grande quanto as outras regiões da América do Sul. Áreas de vida de machos são maiores do que as áreas de fêmeas e a área de vida aumenta com o aumento do peso de machos. O gato-do-mato seleciona floresta durante todo o dia. Arrozais, áreas úmidas e entorno de casas de fazendas foram selecionados no período noturno e evitados na fase clara do dia. Pastagens são sempre evitadas.

5. Todos os impulsionadores de mudanças da dieta levaram à substituição de espécies de presas ao longo dos gradientes biogeográficos e antropogénico. Limitações físicas e biológicas da paisagem podem explicar essas mudanças. A especialização da dieta foi correlacionada com o consumo de presas grandes, principalmente *Lepus*. Nossos dados reforçam as predições de que este pequeno felino é tolerante quando submetido a habitats antropizados. O uso intenso de áreas manejadas apoia esta afirmação. A floresta ripária e áreas úmidas são essenciais para o gato-do-mato nas paisagens modificadas pelo homem no extremo sul do Brasil.

Palavras-chave: altitude, seleção de hábitat, área de vida, latitude, *Leopardus geoffroyi*, Bioma Pampa

General Introduction

Mammalian carnivores are among the species that shape habitats by top-down control. They consume and scare several prey species, therefore indirectly affecting plants and abiotic processes through trophic cascades (Abrams 1992, Schmitz et al. 2000, Thébault & Loreau 2003, Suraci et al. 2016). This influence becomes evident when the top predators are absent in the ecosystem (e.g. Beschta & Ripple 2008). In contrast, the habitat attributes impose limitations and provide ways to carnivores perform their ecological function (Tews et al. 2004). The increase of habitat heterogeneity leads to diversity of interactions (Stein et al. 2014) and the predator-prey relationship resulting are the clearest example of this complex connections (Menge & Sutherland 1976). The great variation on landscape structure can bring forth different predator behavior patterns (e.g. Iriarte et al. 1990, Oliveira 2002). Thus, exploring how shifts in habitat structure affect aspects of carnivore life-history is essential to understand its ecological role in ecosystems (e.g. Virgós et al. 1999, Zhou et al. 2011).

However, the constant natural habitat loss results in several negative changes to ecological processes (Hoffmann et al. 2010, Wilson et al. 2016). Consequently, the human-induced modifications has been the main global threats to carnivores species (Cardillo et al. 2004, Ripple et al. 2014). The predator's natural low density, trophic specialization and human conflicts amplifies the threats (Crooks 2002). The Neotropical wild cats are included in this context (Oliveira 1994, MacDonald et al. 2010). But the continuous structural and functional landscape changes lead these predators to a new background of needs and constraints (e.g. Pereira et al. 2006, 2012, Pereira & Novaro 2014, Castillo et al. 2019). Consequently, it allows them to express all their adaptability to persist in these human-modified ecosystems.

Among the Neotropical wild cats the Geoffroy´s cat *Leopardus geoffroyi* (d'Orbigny & Gervais 1844) is a high adaptivity small cat (3-5 kg, Oliveira & Cassaro 2015) that inhabits a varied number of environments types including wetlands, dry forests, grasslands, scrublands, and disturbed areas such livestock ranches and rice fields (Cuellar et al. 2006, Perovic & Pereira 2006, Pereira et al. 2012). It uses both open and closed habitats from arid and high elevations (3.800 m h.a.s.l) to humid coastal plains (Pereira et al. 2015). Even being one of the small cats with the most available data in South America, the ecological processes behind its adaptability to constant habitat changes are still unclear (Castillo et al. 2019).

Understanding how Geoffroy´s cat deals with natural and human-induced environmental shifts from large to small scale would enlighten its adaptability power and help design further conservation actions for this species. In this way, we conducted two studies concerning Geoffroy´s cat ecological aspects. The study was split into two chapters. In the first, we investigate the large-scale effects of the latitudinal, altitudinal and human disturbance gradients on three aspects of the Geoffroy diet: diet structure, specialization and mean mammal prey size. In the second, we consider other three aspects to understand the adaptive behavior of this small cats in small-scale context on human-modified area in southern Brazil: home range size, habitat selection and activity pattern. We performed a meta analyses and Structural Equation modelling to diet assessment and GPS technology to evaluate the biological features on small-scale.

Chapter 1. Latitude, altitude and human disturbance drive turnover in diet of Geoffroy´s Cat

Abstract

1. Mammalian carnivores exert direct and indirect effects on communities through top-down control. In this context, trophic ecology studies are crucial to understand the ecological processes behind these interactions. But most diet studies reveal only local patterns. Large-scale biogeographic and anthropogenic drivers can also change on carnivore diet patterns. We investigate how the latitude, altitude and human disturbance drive changes in Geoffroy´s cat diet on large geographical scale.

2. Twenty articles addressing diet composition were reviewed. We measured prey consumption of Geoffroy´s cat in different sites to estimate the effects of drivers in three diet descriptor variables: diet structure, specialization and mean mammal prey size.

3. We explore how environmental and anthropogenic drivers affect these three components and how they are linked. We used a Structural Equation modelling to test our hypothesized relations. The model provides an integrative perspective on the role of latitude, altitude and human disturbances in the Geoffroy´s cat diet.

4. Our results uncover a preference for prey around 300 g in large geographical scale, such as *Ctenomys* and *Cavia*. All drivers caused turnover of prey species in diet structure. The increase in latitude degrees leads to higher diet specialization and larger prey selection. Higher altitudes and intensification of human disturbances drives to lower diet specialization and smaller target prey-size.

5. The latitude, human disturbance and especially altitude are determinant drivers of Geoffroy´s cat diet across South America. Diet specialization was correlated with consumption of large prey, mainly *Lepus* consumption.

Key-words: feeding ecology, Neotropical cat, *Leopardus geoffroyi*, predator-prey relationship, Structural Equation Modeling.

Resumo

1. Os mamíferos carnívoros exercem efeitos diretos e indiretos nas comunidades através do controle ‘top-down’. Neste contexto, estudos que abordam ecologia trófica são cruciais para compreender os processos ecológicos por trás dessas interações. Mas a maioria dos estudos de dieta revela apenas padrões locais. Os fatores biogeográficos e antropogênicos em larga escala também podem mudar os padrões da dieta de mamíferos carnívoros. Investigamos como a latitude, altitude e perturbação humana provocam mudanças na dieta dos gatos em grande escala geográfica.
2. Vinte artigos sobre a composição da dieta foram revisados. Foi medido o consumo de presas do gato-do-mato *Leopardus geoffroyi* em diferentes locais para estimar os efeitos dos impulsionadores de mudanças em três variáveis descritoras da dieta: estrutura da dieta, especialização e tamanho médio do mamífero presa.
3. Nós exploramos como os impulsionadores ambientais e antropogênicos afetam esses três componentes e como eles estão ligados. Usamos uma modelagem de Equação Estrutural para testar nossas hipóteses. O modelo fornece uma perspectiva integrativa sobre o papel da latitude, altitude e distúrbios humanos na dieta do gato-do-mato.
4. Os nossos resultados revelam uma preferência por presas de cerca de 300 g ao longo de uma grande escala geográfica, como *Ctenomys* e *Cavia*. Todos os impulsionadores de mudanças causaram a substituição de espécies de presas na estrutura da dieta. O aumento dos graus de latitude leva a uma maior especialização da dieta e maior seleção de presas. Altitudes mais elevadas e a intensificação dos distúrbios humanos conduzem a uma menor especialização alimentar e menor tamanho de presa.
5. A latitude, distúrbio humano e especialmente a altitude são fatores determinantes da dieta do gato-do-mato em toda América do Sul. A especialização da dieta foi correlacionada com o consumo de grandes presas, principalmente *Lepus*.

Palavras-chave: ecologia alimentar, felino Neotropical, *Leopardus geoffroyi*, relação predador-presa, Modelo de Equação Estrutural.

Introduction

Carnivore's diet is one of the most important components to understand the role this group at different ecological levels. It is the main component in the complex connection between predator-prey and how these elements contribute to the dynamic balance of communities (Gittleman 1989, Mills et al. 1993, Terraube & Arroyo 2011). Under this feeding ecology context, carnivores exert a classic controlling influence on species by top-down effect regulation (Gittleman 1989, Estes 1995, Roemer et al. 2009). To explore these interactions is key for designing further research. And, the investigations concerning carnivore´s diet is, first of all, the most usual way for studying this guild.

Many carnivores are rare or elusive species and this makes unraveling trophic relationships very difficult (Davison et al. 2002). Surveying scats, stomach contents and carcass remnants are the easiest methods to reconstruct food consumption on space and time (Putman 1984). Most studies have concentrated on the relative importance of different preys, along with their numbers, prey mass (i.e. biomass, Jaksic 1989a, Ray & Sunquist 2001), or niche breadth (Colwell & Futuyma 1971). Despite the importance of this research, they do not reveal wide patters of trophic interactions. Commonly prey species and its abundance changes over carnivores' distribution and so should carnivore diet (Gittleman 1989, Roff 2002). Food abundance and availability are one of the main drivers to dietary constraints (Pyke et al. 1977, Sundell et al. 2003), especially for a carnivore with specialist food habits (Futuyma & Moreno 1988, Estes et al. 2003, Terraube & Arroyo 2011). Besides, the diet can change between different populations of due to habitat and social constraints (Bekoff et al. 1984, Futuyma & Moreno 1988, Gittleman 1989). Hence, it is challenge to determine what explains these geographical variations in diet.

From this perspective, environmental features may help understand the differences in diet structure. The great variation on landscape structure can generate different patterns on diet composition (Iriarte et al. 1990, Oliveira 2002). Furthermore, elements affecting prey choice by predators usually differ across landscapes, and this knowledge is fundamental to determine the ability of predators to deal with different prey availabities and habitat characteristics (Sunquist & Sunquist 1989). One of the factors that has been used to explain trophic variability is latitude, with a general prediction that lower latitudes have high diet diversity (Fischer 1960, Pianka 1966, Schall & Pianka 1978, Hillebrand 2004). Other factors, such as altitude (Patterson et al. 1989, Stevens 1989, Field et al. 2009, Hartova-Nentvichova et al. 2010) and human disturbances (Dumond et al. 2001, Foster et al. 2009, Pereira et al. 2012) also promote changes. In general, the species diversity decreases at higher altitudes (Rosenzweig 1995), the complexity of predator-prey interaction is also lower. However, human disturbances are among the processes that most affect community structures (Crooks 2002, Mcdonald et al. 2008, Crooks et al. 2010, Haswell et al. 2017). Human presence directly and indirectly affects wildlife, especially larger species that are hunted (Price & Gittleman 2007, Brodie et al. 2015). It can great changes on carnivore prey diversity and availability (Kerley et al. 2002, Havlick 2004, Farias & Kittlein 2008, Rubio et al. 2013). Thus, human disturbance, altitude and latitude are likely influences on carnivore diet along geographical scale.

There might be many environmental features that influence carnivore diet, but it does not detract for carnivores’ ability to occupy a wide array of habitats (Rosenzweig 1995, Lewis et al. 2015). Widening or restricting the prey spectrum and targeting larger or smaller prey are predator responses to environmental and anthropogenic changes

(Futuyma & Moreno 1988, Fraschina et al. 2014) that allow carnivores to persist in different habitats.

Neotropical small wild cats may shed some light in the importance of each of these environmental features on carnivore diet. These mesopredators play a basal role for structuring prey life-history on tropical and sub-tropical ecosystems of South America (Oliveira 1994, Sunquist & Sunquist 2002). Geoffroy´s cat *Leopardus geoffroyi* (d'Orbigny & Gervais 1844) is one of these carnivores and considered a specialist species in its feeding habits (Sunquist & Sunquist 2002). This small cat is a highly adaptive species, inhabiting a wide variety of habitats including wetlands, dry forests, grasslands, scrublands, and disturbed areas such livestock pastures and rice fields (Cuellar et al. 2006, Perovic & Pereira 2006, Pereira et al. 2012). It uses both open and covered habitats and most of its distribution is in arid or semi-arid regions (Pereira et al. 2006). Its diet is mainly composed of small mammals (especially rodents), followed by small birds and minor reptiles (Novaro et al. 2000, Manfredi et al. 2004, Bisceglia et al. 2008, Trigo et al. 2013, Kasper et al. 2016, Guidobono et al. 2016). However, this small cat shows flexibility on prey consumption, taking large mammals (Johnson & Franklin 1991, Branch 1995, Sousa & Bager 2008) and large birds (Canepuccia et al. 2007). Very few studies have dealt with extensive comparisons Geoffroy´s cat diet (e.g. Bisceglia 2014) and only one suggested change its diet over a geographic variation, in a small range (Manfredi et al. 2004). It is clear that large scale drives of Geoffroy´s cat diet changes are still unknown.

Here, we studied three aspects of this carnivore diet in a large geographical scale, which depicts different descriptors of carnivory: diet structure, mammal prey biomass, and diet specialization. We investigate how environmental and anthropogenic drivers affect these three components, as well as how they are linked. We used a

Structural Equation Modelling to test our hypothesized relations, and to control for collinearity among environmental and anthropogenic drivers. Following the driver's general predictions and for being a carnivore specialist but feeding opportunistic, we expect changes in Geoffroy´s cat diet structure in latitudinal, altitudinal and human disturbance gradient. As a consequence, the diet specialization and mammals prey size also switch in this contrasting contexts.

Methods

Study area

The study area covers the whole area of Geoffroy's Cat distribution. *Leopardus geoffroyi* occurs in South-central of South America, from Uruguay and southern Brazil to Andean region of Bolivia and northern Argentina, covering also the Chaco region in Western Paraguay and Argentina to the whole Patagonia, including the South Chilean, from sea level to 3800m (Cabrera 1957, Ximenez 1975, Pereira et al. 2015).

Literature review

The literature search yielded 20 studies in 17 areas from three countries (Table 1). We try to include as many studies as possible, but relevant studies were selected based on the following criteria: (a) diet composition was estimated by an analysis of scats and/or stomachs; (b) taxonomic groups were described at least at the family level; and (c) the place and time span of the study were reported. Twelve studies were conducted within protected areas and the others were conducted in private areas.

Table 1. References used to describe Geoffroy´s cat diet reviewed in this paper.

Reference	**Country**	**Latitude**	**Longitude**	**Mean altitude (m)**	**Method**	**Scats/Stomach number**
Bisceglia et al. 2008	Argentina	37	65	330	Scats	182
Guidobono et al. 2016	Argentina	34	59	20	Scats	494
Johnson & Franklin 1991	Chile	51	72	110	Scats	325
Kasper et al. 2016	Brasil	30	54	100	Stomach	14
Meiorin & Kasper 2005	Brasil	30	54	100	Stomach	6
Pereira et al. 2012	Argentina	37	65	330	Scats	258
Souza & Barger 2008	Brasil	30	52	87	Scats	75
Trigo et al. 2013	Brasil	30	54	100	Stomach	17
Araya 2011	Argentina	36	56	1	Scats	225
Canepuccia 1999	Argentina	37	57	3	Scats	119
Costilla 2010	Argentina	38	62	8	Scats	68
Novaro et al. 2000	Argentina	40	71	1015	Scats and Stomach	36
Palacios et al. 2012	Argentina	37	68	850	Scats	92
Vuillermoz 2001	Argentina	36	56	1	Scats	120
Alvarez 2011	Argentina	36	64	135	Scats	24
Manfredi et al. 2004 (a)*	Argentina	37	57	1	Scats	117
Manfredi et al. 2004 (b)*	Argentina	38	62	205	Scats	184
Bisceglia 2014	Argentina	37	65	330	Scats	148
Migliorin et al. 2018	Brasil	30	54	100	Stomach	37
Berg 2007	Argentina	36	68	1650	Scats	88

* Manfredi et al. 2004: (a) Campos del Tuyú Wildlife Reserve, northeastern of Buenos Aires province; (b) Ernesto Torquist Provincial Park, southwest of Buenos Aires province.

We define ‘diet’ as the relative proportions variety of food ingested, controlling for biases problems particular of each method (Balestrieri & Prigioni 2011, Klare et al. 2011). The majority of the studies focused on descriptive aspects of diet such as diet composition and feeding habits. Most studies focused on the seasonal variation of diet and describe in detail aspects of the diet, such as prey availability on environment (Vuillermoz 2001, Berg 2007, Costilla 2010, Bisceglia 2014, Guidobono et al. 2016). Some studies were conducted on the same area in Argentina, but in different times (Bisceglia et al. 2008, Pereira et al. 2012 and Bisceglia 2014 from Lihue Calel National Park, Vuillermoz 2001 and Araya 2011 from Campos del Tuyú Wildlife Reserve). Despite the of the spatial correlation we consider them independent studies. Some studies from Rio Grande do Sul state, Brazil had a similar problem (Trigo et al. 2013, Meiorin & Kasper 2005 and Kasper et al. 2016), They were inaccurate when describing the study area, giving a toponym that describe a very large region of the state. In this case, we extract a central coordinate between all sample locations. Manfredi et al. (2004) analyzed three areas, but we only consider two of the three, because the third (Mar Chiquita Biosphere Reserve, southeastern of Buenos Aires province) is the same data from Canepuccia (1999). Berg (2007) combined scats from *Oncifelis* spp. (*O. geoffroyi* = *Leopardus geoffroyi* and *O. colocolo* = *L. colocolo*), but we consider the Berg´s data as *L. geoffroyi*.

Analysis procedures

To determine the main descriptor for analysis we extracted the percentage of occurrence (PO) of each prey item or taxon added. The PO described as the total number of occurrences of each food item recovered from scats or stomachs was divided by the total number of items identified across all samples (Reynolds & Aebischer 1991). When the number of items were not explicitly described we obtained from the data available. The only exception was Bisceglia (2014), that we used frequency of occurrence because it was not possible to extract the PO with the available information.

We combine species of the same genus and updated the taxonomic nomenclature (especially for the Caviidae family). The other categories of prey species were aggregated only by higher taxonomic level: e.g. Birds, Reptiles, Amphibians, and Invertebrates. The carrion of livestock, plants and others items category were not considered in analyzes. Mammals prey mass was obtained from Redford & Eisenberg (1992) and Eisenberg & Redford (1999). The geographical location (latitude and altitude) and altitude of the 20 areas studied was obtained from original source data. When the precise locations were not available, the information were extracted from detailed maps (Google Earth©). To calculation the human disturbance levels of each site we used Human Footprint Index (WCS & CIESIN 2005). This index can be summarized as a composite of human population and infrastructure data.

To observe changes in PO of prey´s classes (Mammals, Birds, Reptiles, Fishes, Amphibians and mammalian genus) at different sites along latitudinal, altitudinal and human disturbance gradient we performed an indirect ordination to sort prey taxon by environmental gradient. Due the importance of mammals´ as the main prey to Geoffroy´s cat diet we lead the principal analysis only this taxon, described below.

Diet descriptors

The Geoffroy´s cat diet was described in three aspects: diet composition, mean mammal prey size and degrees of specialization. The diet composition was represented by two axes of indirect ordination performed by non-metric multidimensional scaling (NMDS) on the basis of a Bray-Curtis dissimilarity matrix. The biological meaning (prey) of each axis (MDS1 and MDS2) was estimated by observing Pearson's correlation between the PO of each taxon-prey and the axis. The mean of mammal prey size of each site was estimated through the mean weight of the taxon-prey found in the Geoffroy´s cat diet at that site, pondered by their respective PO.

The *L. geoffroyi* specialization degrees in each location was obtained through the *D* index of specialization (Blüthgen et al. 2006). And since our analysis involves this only one predator and several groups of prey, we need to use an individual web approach to estimate the *D* index in a bipartite framework. In this case, each study was characterized as an "individual" of Geoffroy´s cat, permitting the construction of the bipartite web and the calculation of specialization associated with the individual node (here a described diet of each location). The *D* index is derived from Shannon's entropy and considers the possible and performed interactions, ranging from 0 (completely generalist individual) to 1 (completely specialist individual). The NMDS analyses, mean of mammal prey size, and specialization were done within the R environment, using the *vegan, base* and *bipartite* packages respectively (Core Team 2017).

Structural equations analysis

To evaluate the direct and indirect effects of latitude, altitude and human disturbances on the three aspects of diet, and the relationships between these aspects, we used a Structural Equations Modelling (SEM). About structuring the equations, we hypothesize linear causal relationships of latitude, altitude, and human disturbances on the three aspects of diet. In addition, we also consider that changes in diet composition could direct changes in mean of mammal prey size and/or degrees of specialization. Finally, we evaluate if the degrees of specialization should drive changes in the mean of mammal prey size. The structural equations were performed in R environment using the *lava* package.

Results

Description of diet composition

Mammals proved to be the main food categories eaten by Geoffroy´s cat across all studies considered in this review, representing 76.4 (± 14.9) % of consumed items. Birds represent a secondary food 16.9 (±16.3) %, while reptiles and invertebrates were a complementary prey in Geoffroy´s cat diet, 2.2 (±6.6) % and 1.4 (±5.4) respectively. Amphibious and Fishes can be categorized as eventual food and provide low contribution in large scale (< 0.5 %). The adult mammal prey mass varied between 12 g and 120 kg (mean 4461,9 g ± 18080,9 g), but excluding species over 10 kg (probably carcass consumption) the mean declines to 768,3 g (±1661,4 g).

The latitudinal and altitudinal variation promotes different percentage of occurrence (PO) of prey categories on Geoffroy´s cat diet (Fig.1). Mammals are important prey over all range and birds increase on middle latitude and altitude degrees. Sites without or with reduced reptile’s occurrence overlap with high bird´s occurrence. The reptiles and invertebrates higher in southern latitudes while amphibious and fishes are present at northern latitudes. We find that birds increase with human disturbance contrary to reptiles and invertebrates. The percentage of mammals was not influenced by human disturbance, neither were amphibious or fishes.

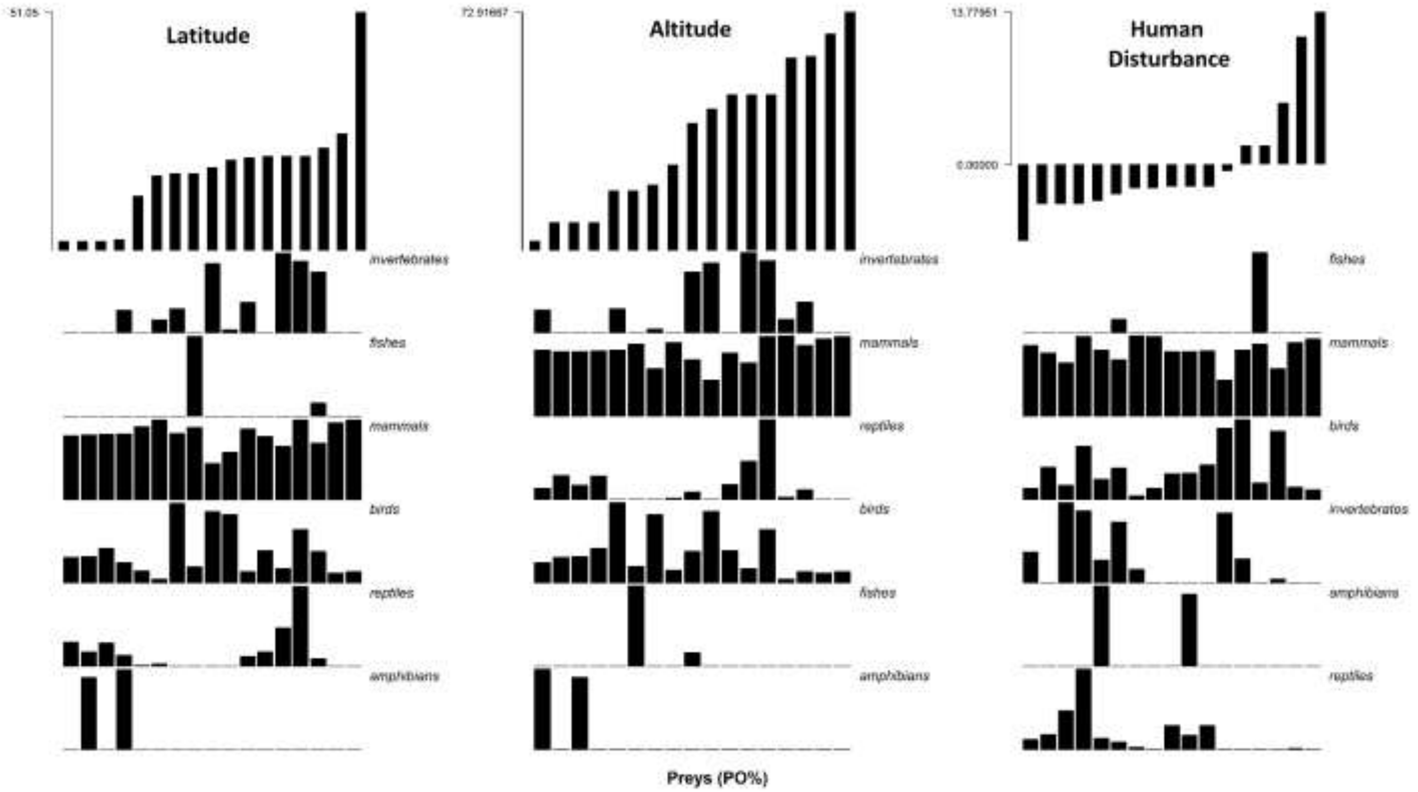

Fig. 1 – Changes on *Leopardus geoffroyi* prey percentage of occurrence across latitudinal, altitudinal and human disturbance variation on South America.

Mammalian prey species across latitudinal, altitudinal and human disturbance gradient

When focusing only mammal prey we find a latitudinal, altitudinal and human disturbance gradient (Fig. 2). There is a clear turnover on prey species across Geoffroy´s cat range. With increasing latitude and altitude there is a *Cavia* by *Ctenomys* replaces *Cavia*, *Reithrodon* replaced *Holochilus* and *Dolichotis replaces Myocastor*. In contrast, some species are present throughout the studied sites, but still show latitudinal and altitudinal trends in their selection (i.e. PO changes), for example, *Oligoryzomys* by *Akodon* (Fig. 2 A, B). However, there is no clear species turnover with increased human disturbance human disturbance (Fig. 2 C). A small number of species are directly associated with high disturbance, while other are not sensible to human disturbance. Overall, the consumption of most prey species is associated with medium and low disturbances.

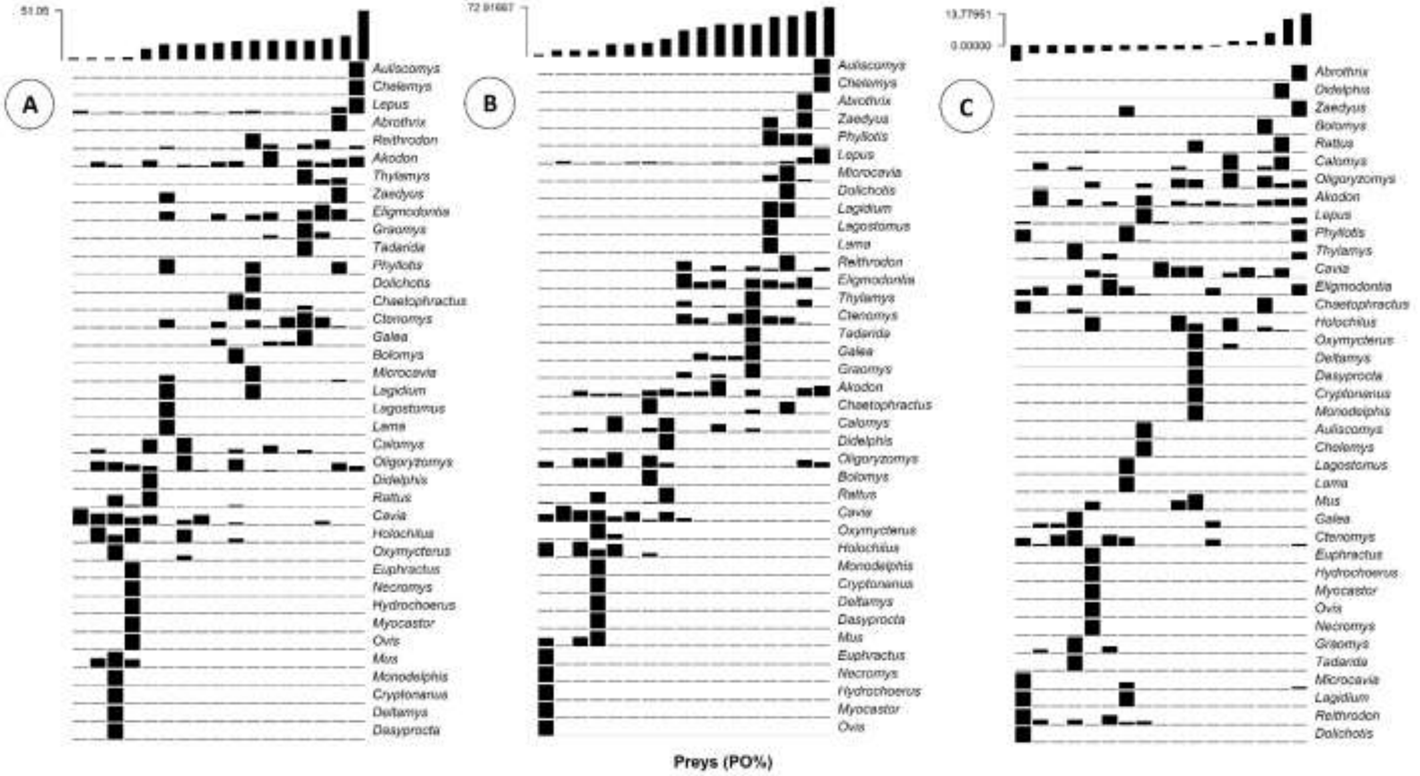

Fig. 2 – Changes on percentage of occurrence of *Leopardus geoffroyi* mammal prey across latitudinal (A), altitudinal (B) and human disturbance (C) variation on South America.

Ctenomys spp. and *Cavia* spp. (±300 g) were the most important food for Geoffroy´s cat throughout their range, especially on low and middle latitudes. Hare (*Lepus* spp., 2900 g) consumption is higher as both latitude and altitude increase. Among all species of Cricetidae family we find genus that are determinant to *L. geoffroyi* across it range, in importance order: *Oligoryzomys*, *Calomys, Akodon, Holochilus* and *Eligmodontia* (Fig. 3). We find that diet specialization lower as altitude and altitude decrease.

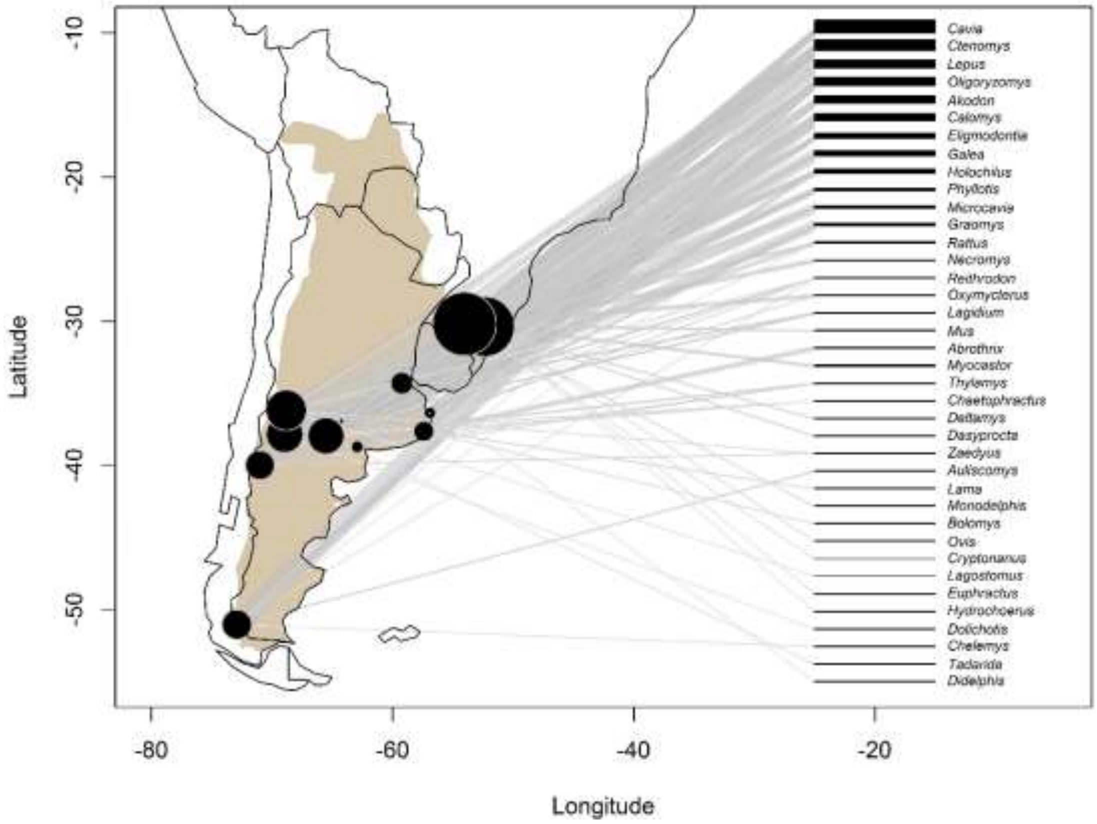

Fig. 3 – Geographical distribution of *Leopardus geoffroyi* on South America (brown area, Pereira et al. 2015) and its mammal prey web interaction. The right column shows prey groups and bar sizes represent the percentage of prey occurrence in the total diet. Black circles illustrate the 20 reviewed studies and their circumference size represents the number of occurrences of each study (rises with decreasing diet specialization degrees). Gray lines represent which prey groups were found in each site.

Biogeographical and anthropogenic drivers

The causal structure predicted and estimated in the SEM recovery adequately the variance-covariance matrix observed in the data (Chi-square = 0.05; df = 1; p = 0.81) (Fig. 4). Human disturbance was structured in space, decreasing in higher altitudes (β_1 = - 0.89). Diet structure was driven directly by latitude (β_2 = 0.53), human disturbance (β_3 = 0.44) and mainly altitude (β_4 = - 0.83), where the last also exerted indirect, human disturbance-mediated (β_1 * β_3 = - 0.39), effect on diet (see indirect effects on Table 2). Diets in southern latitudes, high human disturbance, and higher altitudes were dominated by *Ctenomys*, *Eligmodontia*, *Reinthrodon*, *Galea* and *Lagidium* (Table 3). Conversely, northern latitudes, low human disturbance, and lower altitudes presented diet dominated by *Cavia*, *Holochilus*, *Oligorizomy*.

Table 2. Summary of direct and indirect effects of predictors Latitude (Lat), Altitude (Alt) and Human disturbances (HD) on response variables Diet structure (DS), Specialization (Spec) and Mean of mammal prey size. Positive values represent positive effects and vice versa. Total effects are results of effects multiplication.

Response variables	**Drivers**	**Direct effects**	**Partial indirect effects**	**Indirect effects**	**Total effects**
Human Disturbance	Lat	-	-	-	-
	Alt	-0.89	-	-	-0.89
Diet structure (MDS1)	Lat	0.53	-		
	Alt	-0.83	≈HD=-0.39	-	-0.39
	HD	0.44	-	-	-
Specialization	Lat	-	≈MDS1=0.55	0.55	0.55
	Alt	-	≈MDS1=-0.87	-1.28	-1.28
		-	≈HD≈MDS1=-0.41		
	HD	-1.06	≈MDS1=0.46	0.46	-0.60
	DS-MDS1	-1.05	-	-	1.05
Mean of mammal prey size	Lat	-	≈MDS1≈Spe=0.24	0.24	0.24
	Alt	-	≈MDS1≈Spec=-0.38	-0.56	-0.56
		-	≈HD≈MDS1≈Spe=-0.18		
	HD	-	≈Spe=-0.46	-0.26	-0.26
		-	≈MDS1≈Spe=0.20		
	DS-MDS1	-	≈Spe=0.46	0.46	0.46
	DS-MDS2	-0.46	-	0.46	0.46
	Spe	0.44	-	-	0.44

Table 3. Genus of mammalian prey species consumed by Geoffroy´s cat across geographical distribution, MDS1/MDS2 axes values and the mean of genus mass (Weight). The weight and locomotor habit were obtained from Redford & Eisenberg (1992), Eisenberg & Redford (1999), Reis et al. (2006) and Paglia et al. (2012). The prey species ranking had ordered by negative to positive MDS1 values.

Species (Genus)	Diet structure		Weight	Locomotor habit
	MDS1	MDS2		
Ctenomys	-0.824865407	-0.034232981	350	semi-fossorial
Eligmodontia	-0.672356009	0.15443514	19	cursorial
Reithrodon	-0.502531546	-0.133454598	81	semi-fossorial
Galea	-0.472802326	0.362458915	400	cursorial
Lagidium	-0.471916191	-0.386962753	1500	cursorial
Phyllotis	-0.447651145	-0.298080906	57	cursorial
Microcavia	-0.418049966	-0.37957291	300	cursorial
Graomys	-0.355953014	0.299590853	63	cursorial
Lama	-0.353112109	-0.213146295	120000	cursorial
Lagostomus	-0.353112109	-0.213146295	5200	semi-fossorial
Thylamys	-0.335593829	0.251883837	25	cursorial
Dolichotis	-0.292128557	-0.318667941	8000	cursorial
Tadarida	-0.262639876	0.251285098	11,5	volant
Zaedyus	-0.246723675	-0.071198003	1000	fossorial
Chaetophractus	-0.100743439	0.064961065	1320	semi-fossorial
Akodon	-0.080497042	0.743933583	36	cursorial
Abrothrix	-0.052436215	0.059033193	20	cursorial
Lepus	0.028035917	0.063551596	2900	cursorial
Auliscomys	0.039323765	0.15852647	73	semi-fossorial
Chelemys	0.039323765	0.15852647	71	cursorial
Bolomys	0.170850551	0.266235594	35	cursorial
Didelphis	0.174172429	0.13817365	1560	scansorial
Cryptonanus	0.279003982	-0.115305828	30	arboreal
Monodelphis	0.279003982	-0.115305828	45	semi-fossorial
Deltamys	0.279003982	-0.115305828	26	semi-aquatic
Dasyprocta	0.279003982	-0.115305828	3000	cursorial
Calomys	0.310675201	0.565433813	24	cursorial
Rattus	0.346379017	0.054098324	275	cursorial
Oxymycterus	0.351300683	-0.02217459	75	cursorial
Euphractus	0.409442888	-0.075146911	4680	semi-fossorial
Necromys	0.409442888	-0.075146911	35	cursorial
Hydrochoerus	0.409442888	-0.075146911	45000	semi-aquatic
Myocastor	0.409442888	-0.075146911	6400	semi-aquatic
Ovis	0.409442888	-0.075146911	70000	cursorial
Mus	0.527911603	-0.102378149	20	cursorial
Oligoryzomys	0.674344531	0.428234521	22	scansorial
Holochilus	0.678002841	0.165055333	170	semi-aquatic
Cavia	0.722262638	-0.472195052	350	terrestrial

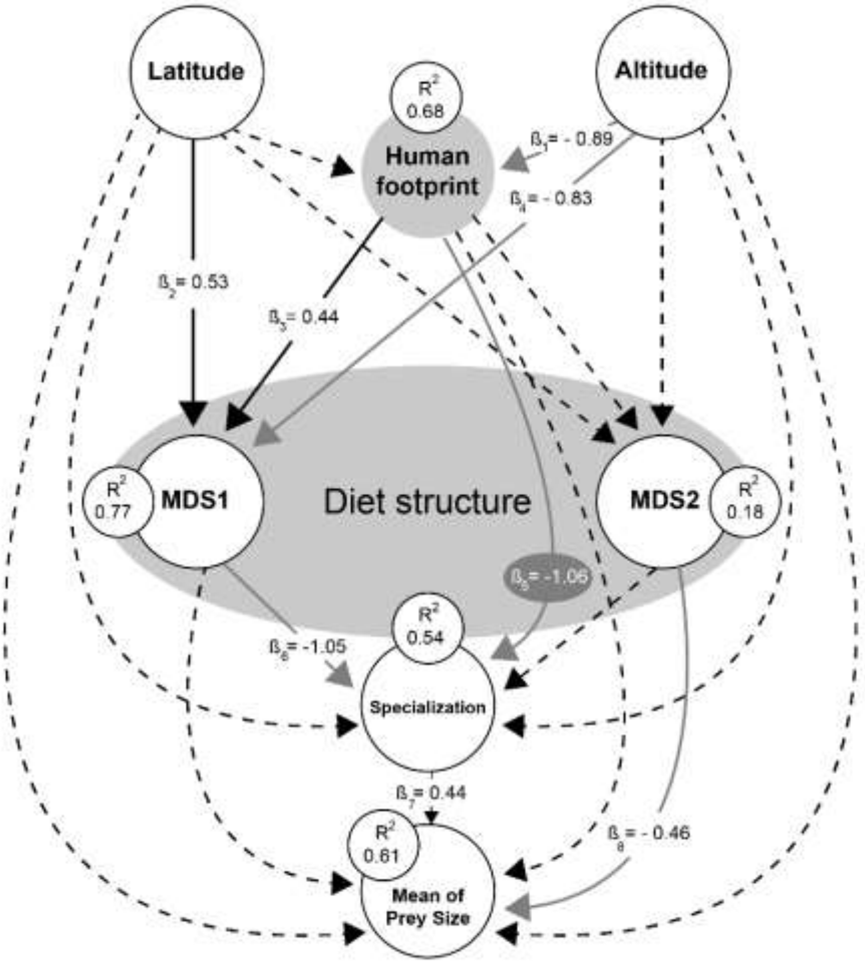

Fig. 4 – Interaction among the predictors latitude, altitude and human disturbance and the response variables, diet structure (MDS1 and MDS2), specialization and mean of mammal prey size (prey size) of *Leopardus geoffroyi* diet. Positive effects are indicated by black arrows and negative effects by gray arrows. Dashed arrows indicate non-significant effects ($p \geq 0.05$). The standardized coefficients (β) represent the relative strength of effects. β_1 to β_8 are coefficients of linear regressions. R^2 represent the explanatory power of each variable.

Diet specialization had direct effect from human disturbance (β_5 = - 1.06), but not of latitude and altitude. Diets in disturbed areas were more generalist than in those more pristine. Although, latitude and altitude lack direct effect on specialization, they exerted indirect effects ($\beta_{total\ indirect}$ for latitude [0.55] and altitude [-1.28]) mediated by driving human disturbance and diet structure. At this case, northern latitudes, and mainly, higher altitudes promoted more generalist diets. Mean prey size was only driven by the degree specialization, which more specialized diets were concentrated in larger preys (β_7 = 0.44). Once again, latitude ($\beta_{total\ indirect}$ = 0.24), human disturbance ($\beta_{total\ indirect}$ = - 0.26) and altitude ($\beta_{total\ indirect}$ = - 0.56) presented only indirect effects by mediating diet structure and specialization. Southern latitudes, lower altitudes and less disturbed areas promote more generalist diets.

Discussion

Geoffroy´s cat adaptive diet

Small mammals are the most important prey for Geoffroy´s cat across its range distribution. However, this carnivore seems to consume prey opportunistically according to its availability (Manfredi et al. 2004). Supporting that, most of studies that evaluated small-scale diet composition and prey availability showed this pattern, for which a small carnivore with specialized diet consumes its prey in an opportunistic manner (Manfredi et al. 2004, Canepuccia et al. 2007, Bisceglia et al. 2011).

In general, all wild cats focus their diet at a narrow prey spectrum, often associated with the prey-size (Futuyma & Moreno 1988, Gittleman 1995). To understand the influence of the drivers in the prey size, we will use the biological concept of “preferred prey” (see Clements et al. 2014). Preferred preys are prey who represent a good balance in prey abundance, capture capacity and handling (e. g. Hayward et al. 2006, 2012).

Independently of the latitudinal, altitudinal and human disturbance gradient, the Geoffroy´s cat maintained a high prevalence of mammal prey species around 300g (*Ctenomys* and *Cavia*, especially), suggesting that is Geoffroy´s cat preferred prey size. Predation of species this size appears to be within Geoffroy´s cat ability to subjugate the prey, and is thought to have one of the best cost-effectiveness for a carnivore of this body size (Gittleman 1995, MacArthur & Pianka 1966).

Nevertheless, Geoffroy´s cat displays adaptability by consuming prey outside its preferred prey size. It consumes a high proportion of hare (*Lepus* spp.). In most reviewed studies, hares were captured more frequently when alternative prey was not abundant (Johnson and Franklin 1991, Canepuccia 1999, Novaro et al. 2000, Pereira et al. 2006), which suggests that this prey is hard to capture and is not a selected (see Terraube & Arroyo 2011). This lack of preference is supported by the similarity in body size. The body size of Geoffroy´s cat is similar hare size, so it is likely that only the newborn or young is a profitable prey for this carnivore size. Thus, hares are not the preferred prey of Geoffroy´s cat, but it is able to adapt and exploit this prey. Nevertheless, Geoffroy´s cat seems to overcome these difficulties and successfully hunt this species when others are not available, indicating an ability to adapt. One of the ways of Geoffroy´s cat might exploit hares is by using the sit-and-way hunting strategy (Oliveira 1994, Sunquist & Sunquist 2002). This strategy nullifies hares defense based on speed and tortuous movements to escape from predators (e.g. Hodges et al. 2014). Geoffroy´s cat versatility is further evidenced by the fact hares are introduced species. Thus, hare predation is a recent trophic interaction, which should be the result of an adaptive behavior process (Fryxell & Lundberg 1994). It is likely that the Geoffroy´s cat learned that hares do not offer serious difficulty in handling. Therefore, currently hares represents an excellent cost-benefit and show that Geoffroy´s cat is a remarkable opportunistic predator, especially if autochthonous preferred prey size is absent or in low density.

Despite not being the main group of prey, the bird consumption also illustrates this species' opportunism, increasing in the absence of more favored species such as reptiles and invertebrate. In general, the contribution of these secondary and eventual prey should depend on local abundance (see Pereira et al. 2012, Migliorini et al. 2018). Most of the reviewed studies show a lower contribution of numerical and biomass birds than mammals. An exception was observed by Canepuccia (1999), which detected a high bird's occurrence in Geoffroy´s cat diet. Canepuccia (1999) illustrates that Geoffroy´s cat diet is versatile when it needs to be, even though the species show well defined preferences in large-scale.

Another fact is reinforcing *L. geoffroyi* adaptability is occasional consumption of mammals over 10 kg. Our analyses included this mass-size because the authors considered carcasses as prey, but it requires careful evaluation. We suspect these consumptions is mostly carcasses of animals killed by other events, such as trampling and other predators (Vuillermoz 2001, Novaro et al. 2000, Sousa & Bager 2008). Hence, defining animal of this size as "prey" is questionable. Nevertheless, it is reasonable to hypothesize that is animals were eventual newborn or subadult predation indeed preyed. Actually, the contribution of carcasses on small cats' diet is still poorly understood and it is not clear what are the main drivers of this feeding behavior. Despite not finding support in our data, we expect that there will be an increase the carcasses consumption in rise human disturbances, as these changes will lead to more availability of this resource. Irrespective of carcasses or juvenile consumption, the consumption of large mammals only reinforces its flexible feeding behavior across biogeographical and anthropogenic gradients. This begs the question what environmental features drive this diversity.

The effect of drivers

Even comparing the Geoffroy´s cat diet in small-scale, Manfredi et al. (2004) suggested changes on diet composition, but did not reveal which drivers are responsible for this variation. Distinct carnivore populations may exhibit differences in diet composition, reflecting a local variation in resources (e.g. Iriarte et al. 1990, Oliveira 2002, Farias & Kittlein 2008). Under a larger scale analysis, our results show that diet structure is affected by latitude, human disturbance and mainly by altitude.

The increase in latitude had a direct influence on diet structure by replacing the main preys *Cavia*, *Holochilus*, *Oligorizomy* by *Ctenomys*, *Eligmodontia*, *Reinthrodon*, *Galea* and *Lagidium*. And this turnover leads to higher diet specialization and targeting of larger prey in southern latitudes. The diversity of prey communities and abundance of particular species change along the geographic distribution of this widely distributed predator (Oliveira 2002, Lozano et al. 2006, Foster et al. 2009). Generally, prey availability (e. g. prey diversity and abundance) is mediated by several factors associated with latitude, in particular temperature and spatial heterogeneity (Monjeau et al. 2009). As a rule, this availability decreases in southern latitudes (Rosenzweig 1995), which is a decisive factor to clarify the Geoffroy´s cat diet changes. In low prey diversity context, the predator has lower choices and takes any available prey, even an exotic species. The low availability of native prey and increase in Hare (*Lepus* spp.) abundance must be playing a role in Geoffroy´s cat diet (Novaro et al. 2000, 2004, Pereira et al. 2006, Palacios et al. 2012). Geoffroy´s cat benefits from this occurrence and consumes according to availability specializing its diet and focusing on larger prey (e.g. Johnson & Franklin 1991, Novaro et al. 2000, Manfredi et al. 2004).

An alternative explanation for feeding on larger prey at higher latitudes is the effects of Bergmann's rule (Bergmann 1847, see Ashton et al. 2000). Thus, larger Geoffroy´s cat can catch larger prey. However, there is no correlation between body mass and latitude, not supporting Bergmann’s rule for this species (Lucherini et al. 2006, Nascimento 2014). This reinforces the hypothesis that the predation of larger prey in southern latitudes should be associated with the presence and abundance of hares (Johnson & Franklin 1991, Novaro et al. 2000, 2004, Manfredi et al. 2004, Palacios et al. 2012).

In general, it is expected that coexistence with larger predators (especially wild cats) would lead the smaller cat to prey on smaller prey (Moreno et al. 2006, Oliveira et al. 2010), which somewhat conflicts with our data (high hare consumption). The presence of *Puma concolor* could affects the *L. geoffroyi* feeding in southern latitudes compelling this wild cat to target smaller prey (Rosenzweig 1966). But hare consumption by *L. geoffroyi* did not seem to decrease with *P. concolor* presence in southern latitudes (Martínez et al. 2012). A possible explanation to this apparent contradiction is that when larger native prey is available (e. g. Guanaco, *Lama guanicoe*) *Lepus* spp. are secondary items in *P. concolor* diet (Iriarte et al. 1990, Franklin et al. 1999, Martínez et al. 2012). Therefore, the availability of larger prey to *P. concolor* releases hares to smaller predators. Geoffroy´s cat feeding plasticity could have increased its geographic distribution by Hares spreading. Anyhow, this lagomorph represents an important prey for *L. geoffroyi*, especially in southern latitudes.

Altitude effect had the most pronounced effect in our analyses of Geoffroy´s cat diet structure. This small felid exhibit lower diet specialization in higher altitudes. In general, lower altitudes provide more prey options by having increased prey diversity in the environment (Field 2009) even under human disturbance influences (Hartova-

Nentvichova et al. 2010). In contrast, high elevations are analogous to the unproductive environments, where prey items are relatively rare and searching time is longer (Begon et al. 2006). The predator does not have choice to target its consumption to preferred prey, feeding on everything that is available. Thus, the Geoffroy´s cat broadens its feeding range to inhabit high elevations.

Moreover, Geoffroy´s cat targets smaller prey on higher altitudes. The presence and especially the abundance of preferred prey on this gradient should be also decisive factors to diet changes across its geographic distribution. As elevation increase *Cavia*, *Holochilus*, *Oligorizomys* are no longer consumed and *Ctenomys*, *Eligmodontia*, *Reinthrodon*, *Galea*, *Lagidium* arise on diet. But, under indirect human disturbances influences this switch changes slightly (see Bisceglia et al. 2011, Pereira et al. 2012). Therefore, we reinforce that altitudinal gradient is within the most important factors to the structuring of small mammal communities in southern South America (Kelt 1996, Andrade & Monjeau 2014).

Since altitude is crucial to structuring the community, we are compelled to ask why Geoffory´s cat take smaller prey at higher altitudes? The answer is low human presence. Human disturbances are structured in space, more intensive at low altitudes. Human disturbance reduces the *L. geoffroyi* and *P. concolor* overlap occurrence, by decreasing *P. concolor* density or removing it altogether. For this reason, there are more encounters at high altitudes and this discourages the small cat to feed on larger preys (see Moreno et al. 2006). The probable low abundance of shared prey amplifies this interaction (Iriarte et al. 1991, Rau & Jiménez 2002, Foster et al. 2009). And in high elevations *P. concolor* may constrain the habitat use of *L. geoffroyi* and may even kill it (Oliveira & Pereira 2014). Therefore, higher altitudes lead to *L. geoffroyi* takes smaller prey.

Our results also showed that human disturbances affect the Geoffroy´s cat diet specialization. These anthropogenic changes resulted in two feeding paths, one stronger and direct interaction leading to generalist diet and another secondary mediated by diet structure changes. However, the total effects of human disturbances on diet specialization results in widespread feeding that leads to small-size preys. Countryside with higher human disturbance in South America generally have a mosaic of agricultural crops, planted forest, cattle pastures and natural habitats (see examples of reviewed studies: Pereira et al. 2012, Guidobono et al. 2016, Kasper et al. 2016, Tirelli et al. 2018). Most mammalian species that benefit from this mosaic are inside Geoffroy's cat preferred prey-size range (Sousa & Bager 2008, Palacios et al. 2012, Pereira et al. 2012, Guidobono et al. 2016, Kasper et al. 2016) This landscape can generate increased small rodents abundance and diversity (see Pereira et al. 2012, Guidobono et al. 2016). Because it is easily captured providing the trade-off between size and prey number (see Jaksic 1989b). And all these small mammals are within the range of prey widely consumed by Geoffroy´s cat and as result the species are equitably consumption. This context makes diet less specialized in higher human disturbance.

In addition, human disturbances lead to smaller prey consumption. As previously mentioned, human-induced environmental changes can increase the diversity and abundance of small mammals (especially rodents). As a result, smaller prey near of the preferred prey group are broadly available to Geoffroy´s cat. Furthermore, larger mammal prey in more disturbed environments have chance of being preyed by humans and domestic animals, particularly game and damage species (Foster et al. 2009, Henschel et al. 2011). Therefore, this resource is depleted to *L. geoffroyi*. And, the low diet specialization may increase competition with sympatric carnivore species, stirring the competition and increasing negative effects on Geoffroy´s cat populations (Palacios et al.

2012, Kasper et al. 2016). Thus, despite the fact that food habits are affected by many factors, diversity of small mammals increase in low altitudes (Rosenzweig 1995), and is not clear whether the specialized habit is a result of biogeographic factor or a feature of the human disturbance.

This review of feeding ecology studies show that the abundance and availability of preys are an important trait widely reported to Geoffroy´s cat diet. Our results points a large-scale preferred prey-size selection around 300 g, such *Ctenomys* and *Cavia*. These larger small-size mammals are key prey to this carnivore diet, probably because it contributes qualitatively while small rodents numerically. The latitude, human disturbance and especially altitude are important drivers to Geoffroy´s cat diet across South America. Specialization was guided Geoffroy´s cat focusing in large prey, possibly guided by *Lepus* consumption. It also reveals its adaptability when narrow the diet and select larger prey in southern latitudes and higher altitudes. Besides, the effects of human disturbances on diet specialization leads to small-size prey widespread consumption as a consequence of Geoffroy´s cat adaptation power. Finally, we identify a large geographical gap without feeding ecology studies in northern distribution. Further research at the distribution extremes would improve to better understand the role of drivers on large-scale diet changes.

Chapter 2. Home range, habitat selection and activity patterns of Geoffroy´s cat in a human-modified area

Abstract

1. The physical and biological habitat features affect how the mammalian carnivores perform its basic daily activities. Nowadays, they must also deal with new ecosystem human-modified to avoid vanishing. In this context, the Geoffroy´s cat is an excellent model to understand the small predator adaptations that allow them to persist in modified landscapes.

2. Our aim was to investigate ecological aspects of Geoffroy´s cat in a landscape dominated by flooded rice fields, cattle pastures and patches of natural habitats in Pampa ecoregion on southern Brazil. Due to the prey abundance, habitat heterogeneity and human-induced threats, we expect that this wild cat display small home ranges size when compared to other disturbed areas and use human modified open areas solely during the night.

3. We tracked 14 Geoffroy´s cat between January and October 2017. Home ranges sizes were determined by minimum-convex-polygon and Kernel techniques while the habitat selection and activity patterns by Step Selection analysis.

4. Contrary to our predictions, we found large home ranges, as larger as previous studies. Female’s home range are smaller than males’ and bigger males had larger home ranges size than smaller males. Geoffroy´s cat strongly select riparian forest, especially at daylight. It used rice fields and the surronding of farmhouses during the night, but avoided it at daylight. Roads were used to access these rice fields and farmhouses. Cattle pasture was always avoided.

5. Home range sizes were large even when food was abundant and the habitat was heterogenous. The refined tracking data reinforces the predictions that Geoffroy´s cat is tolerant when subjected to human-modified habitats. The use of rice fields and farmhouses supports this statement. Food availability and human threats seem to shape

the crepuscular-nocturnal activity. Riparian forest and water bodies habitats play a fundamental role to Geoffroy´s cat improve its primary needs in human-modified landscape.

Key-words: GPS, *Leopardus geoffroyi*, movement ecology, Pampa biome, Step Selection function.

Resumo

1. As características físicas e biológicas do habitat influenciam a forma como os carnívoros mamíferos realizam as suas atividades diárias básicas. No presente, eles também devem lidar com novos ecossistemas humano-modificados para evitar a extinção. Neste contexto, o gato-do-mato *Leopardus geofforyi* é um excelente modelo para entender as adaptações de pequenos predadores em paisagens modificadas pelo homem.

2. Nosso objetivo foi investigar os aspectos ecológicos do gato-do-mato em uma paisagem dominada por arrozais inundados, pastagens e fragmentos de habitats naturais no bioma Pampa, sul do Brasil. Devido à abundância de presas, heterogeneidade de habitats e ameaças induzidas pelo homem, nós esperamos que este pequeno felino apresente pequenas áreas de vida quando comparado com outras áreas perturbadas e use áreas abertas manejadas exclusivamente durante a noite.

3. Assim, nós rastreamos 14 indivíduos de gato-do-mato entre janeiro e outubro de 2017. Os tamanhos das áreas de vida foram estimados pelas técnicas de mínimo polígono convexo e Kernel, enquanto a seleção do habitat e os padrões de atividade foram determinados pela análise de seleção de passos.

4. Ao contrário das nossas predições, encontramos grandes áreas de vida, tão grandes quanto demostrando em estudos anteriores. A área de vida de fêmeas foi menor do que a de machos e indivíduos machos maiores apresentaram maiores áreas de vida do que machos menores. O gato-do-mato seleciona fortemente a floresta ripária, especialmente durante a fase clara do dia. Ele usou arrozais e o entorno de casas de fazendas durante a noite, mas evitou à luz do dia. As estradas foram usadas para acessar esses os arrozais e casas. As pastagens foram sempre evitadas.

5. Os tamanhos de área de vida são grandes, mesmo abundância de presas e habitat heterogêneo. Os dados refinados obtidos por meios do rastreamento reforçam as previsões de que o gato-do-mato tolera habitats manejados pelo homem. O uso de arrozais e entorno de casas de fazendas apoia esta afirmação. A disponibilidade de presas e as ameaças humanas parecem moldar a sua atividade crepuscular-noturna. A floresta ripária e as áreas úmidas são fundamentais para o gato-do-mato cumprir suas necessidades primárias em paisagens modificadas pelo homem no sul do Brasil.

Palavras-chave: GPS, *Leopardus geoffroyi*, ecologia do movimento, Bioma Pampa, análise de seleção de passos.

Introduction

Terrestrial mammalian carnivores have needs and constraints that require them to use the space optimally (McNab 1963, Gittleman & Harvey 1982, Jetz et al. 2004, Carbone et al. 2007). The physical and biological habitat features affect how the carnivore will perform its basic daily activities (Beltrán & Delibes 1994, Carbone et al. 1999). For example, heterogeneous and structurally complex habitats provide shelters, prey abundance and can attenuate the negative effects of competitors coexistence (Fedriani et al. 1999, Pereira et al. 2012, Monterroso et al. 2013). In pristine habitats, carnivores play their ecological role without need to deal with human threats. And it can avoid natural threats mainly by temporal and spatial habitat segregation (Gittleman 2001, Di Bitetti et al. 2010, Santos et al. 2013). Thus, biological and structural features of a conserved habitat are essential references for understanding how carnivores deal with new context of habitat changes (Gittleman 2001, Mitchell & Hebblewhite 2012).

The continuous increase in human population has impacted many environments around the world leading to locally extinction of several species (McKinney 2002, Cardillo et al. 2005). Those which remain in human-modified environment had to change their behavior to supply their elementary requirements (Sálek et al. 2015). Behavior changes and flexible resource needs enabled medium-sized carnivores to persist in human-modified landscapes. Most of these behavior changes are in the form of spatial and temporal changes in habitat use (Markovchick-Nicholls et al. 2008, Smith et al. 2018).

By nature or by human intervention, most Neotropical predators are constantly confronted with new scenarios, limitations, opportunities. The Geoffroy´s cat, *Leopardus geoffroyi* (d'Orbigny & Gervais 1844), is an excellent example of this confrontation (Castillo et al. 2008, Pereira et al. 2006, 2012, Manfredi et al. 2012, Caruso et al. 2016). It is one of the most common and widely distributed felids in Southern South America (Sunquist & Sunquist 2002). This small cat is highly adaptive, inhabiting a wide variety of habitat types including wetlands, dry forests, grasslands, scrublands, and disturbed areas such livestock and rice fields (Cuellar et al. 2006, Pereira et al. 2012). It uses both open and closed habitats. In Brazil, it occurs on the Pampa ecoregion in the Rio Grande do Sul state (Cuyckens et al. 2016) and most of its range is found in arid or semi-arid regions of South America (Pereira et al. 2006).

Most Geoffroy´s cat populations outside of protected areas in south of Brazil are exposed to some level of human interference (see Kasper et al. 2016, Tirelli et al. 2018). The clearest modifications are caused by the conversion of natural habitats to cattle ranching and grain plantations (rice, soybeans, corn, especially). This practice is common throughout Geoffroy´s cat range, because these areas were originally open habitats and this conversion could be easily implemented (see Oliveira et al. 2017). In addition to landscape conversion, many other negative impacts affect the small cat in anthropogenic landscape, such as vehicle collision, killing by domestic dogs, poaching, poisoning and diseases (Pereira et al. 2010, Uhart et al. 2012, Peters et al. 2016). These threats lead Geoffroy´s cat to the national list of endangered species (Almeida et al. 2013). In spite of these threats and endangerment, Geoffroy´s cat displays some resilience adjusting its diet, habitat use and activity to new contexts (Pereira & Novaro 2004, Manfredi et al. 2006, 2012, Castillo et al. 2008, 2019, Pereira et al. 2011, 2012, Tirelli et al. 2018). To understand what are the basic needs and constraints of the Geoffroy´s cat in human-modified environment and to design further conservation actions for this carnivore (Pereira & Novaro 2014, Tirelli et al. 2018), it is fundamental to reveal how Geoffroy´s cat adapts its behavior. In this way, home range size, habitat selection and activity patterns are basic ecological aspects to comprise the life history of this small wild cat in modified landscape (see Gittleman & Harvey 1982, Moorcroft 2012, Duncan et al. 2015).

These ecological attributes have been studied before and provided important information for Geoffroy´s cat ecology (see Johnson & Franklin 1991, Manfredi et al. 2006, 2012, Castillo et al. 2008, 2019; Pereira et al., 2006, 2012, Tirelli et al. 2018). Even so, there are still gaps on the Geoffroy´s cat spatial ecology in human-modified environments. Besides, due to the limitation of traditional telemetry method, the previous information should be confronted by more modern techniques. Here, we present a refined data obtained by GPS technology target to uncover the home range size, habitat selection and activity pattern of Geoffroy´s cat in a human-modified habitat on southernmost of Brazil. The habitat heterogeneity and prey abundance lead us to hypothesize that home ranges size is smaller than those in previous studies. Furthermore, we expect that it avoids open human-managed areas during the day light and select mainly native habitats most of the day time We discuss the role of human-induced changes in Geoffroy´s cat adaptive behavior.

Methods

Study area

The study was conducted on coastal fields in Pampa Grasslands of Southern Brazil (Boldrini 2009), Rio Grande do Sul State (31°50'S, 52°54'W, Fig. 1). The study area comprised nearly of 80 km^2 and the landscape is characterized as a mosaic of managed flooded rice fields, cattle pastures (mixed of exotic and native grasses), natural swamps and continuous patches of riparian forest (IBGE 2004). Climate is subtropical humid (*Cfa* in the Köppen climate classification) with wide seasonal variation, hot summers and harsh winters. Mean annual temperature and precipitation is 17.8 ºC and 1259 mm, respectively (Climate-Data.Org 2019). Landscape was historically exploited for agricultural and ranching activity. The natural fields and forests were modified by these practices.

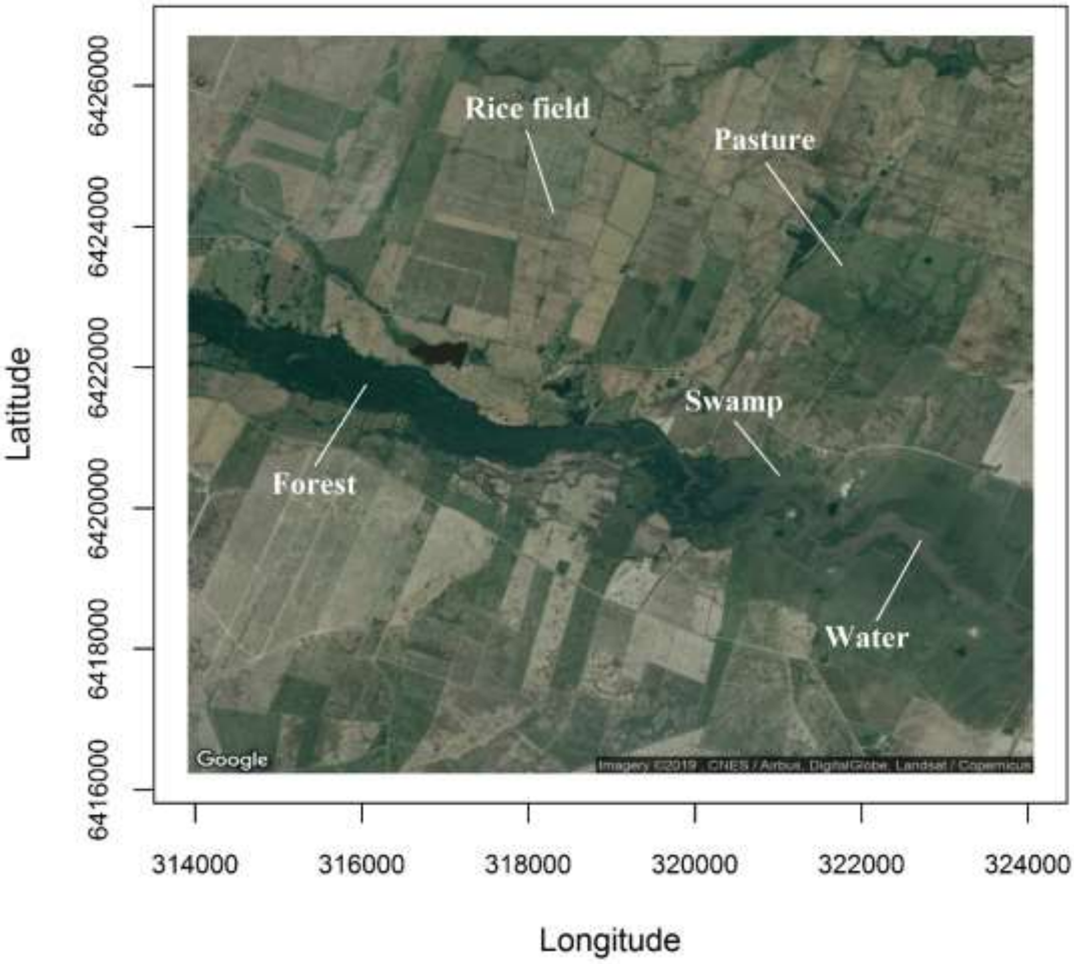

Fig. 1 – Overview of the study area in Pampa biome on southern Brazil. The landscape mosaic consists of pastures, forests, swamps and managed rice fields.

Habitat characterization

We classified the soil land use using Google Earth Pro©. Based on our field experiences, we manually delimited habitat classes within seven categories that had biological meaning for the Geoffroy´s cat: forest, rice fields, swamp, pasture, house, water, and roads. Forest areas are predominantly comprised of riparian forests. Swamps are dominated by *Bromelia* spp. and were often found on edges of the forests. Pasture is characterized by native and exotic grass (*Eragrostis plana*, especially). Rice fields are the only agricultural activity and formed by flooded fields artificially human-managed. Artificial water bodies (irrigation canal), pounds, rivers were included in the water class. The study area is crossed by several unpaved vehicle accesses. All these ways were considered roads.

Capture and tracking methods

Individuals were captured using Tomahawk box traps attached to a live bait wire box (1 cm mesh). The predator can see the bait (domestic doves), but he cannot reach it. The use of live baits was necessary to increase the chances of capturing wild cats and reduce the likelihood of trapping non-target mammals. For the capture and immobilization, we follow the procedures described by Manfredi et al. (2006) and Tirelli et al. (2018). All proceedings were guided by recommendations of Animal Care and Use Committee (1998) and authorized by the Brazilian Ministry of the Environment (permit SISBIO-56373-1). Only healthy adult animals were fitted with GPS-collars (TIGRINUS®), whose weight never exceeded 3 % of individual body mass. Individuals were released at the same place of capture just after recovering from anesthesia. GPS-collars were set to record individual locations every 2 hours, as well as the date and time of the records.

Collars were also set to allow remote data transfer days a month. Downloading was performed using an antenna and a UHF transceiver (TIGRINUS®).

Analysis procedures

Home range

We estimated home range size using Minimum Convex Polygon (MCP100%) (Moht 1947), Kernel Density Estimation (KDE; Worton 1989) and Kernel Brownian Bridge (BRB; Horne et al. 2007). This last one allowed us to incorporate not only relocations, but also the path between successive locations (see details in Horne et al. 2007). Both Kernel estimators were built under a probability isopleth of 95%, the reference smoothing parameter, and diffusion parameter estimated by maximum likelihood. Estimation was carried out in R environment using *adehabitatHR* package.

We tested the effect of sex and body mass, as well as its interaction, on home range size (KDE) using a General Linear Model. We also included the number of relocations in the model for controlling the sampling bias. Furthermore, we assessed the generality of sex effect by including raw information gathered from nine references (MCP100%; Table 1). At this case, we tested the effect of sex using a Mixed Linear Model to include the study identity as random effect. This random effect allowed us to model the sex effect in repeated measure fashion, that means, to check if sex effect is consistent among studies.

Habitat selection and activity pattern

One important issue for habitat selection investigation is to define habitat availability. At a mechanistic viewpoint, habitats available are those placed around the actual organism position, in a buffer that depends on animal navigation and displacement capacity. The method that most closely resembles this logic is the Step Selection Function (SSF, Forester et al. 2009), which requires large amounts of data that only GPS methods can provide. The SSF is an extension of standard Resource Selection Functions that, in turn, take in account movement features to represent changes in habitat availability throughout animal displacement.

Within this framework (SSF), the decision of an individual to move to a habitat type whenever it performs a step could be conditioned on the time of day and on available habitats at alternative locations that the individual could have reached in alternative steps (Thurfjell et al. 2014, Fig. 2). A step is defined as the Euclidian distance between two consecutive relocation fixes. For each observed step, we randomly create 30 alternative steps using Gamma distributions of step lengths and Cauchy distributions of turn angles (i.e. the angular difference between two successive steps, Fortin et al. 2005). Both distributions were adjusted by Maximum Likelihood to the values of step length and turn angles observed in the original trajectory of individuals. The alternative steps, used to represent the available habitats around the animal (control), was compare with the habitat used in the observed step (case) on a matched case-control design (Fortin et al. 2005; Fig. 2).

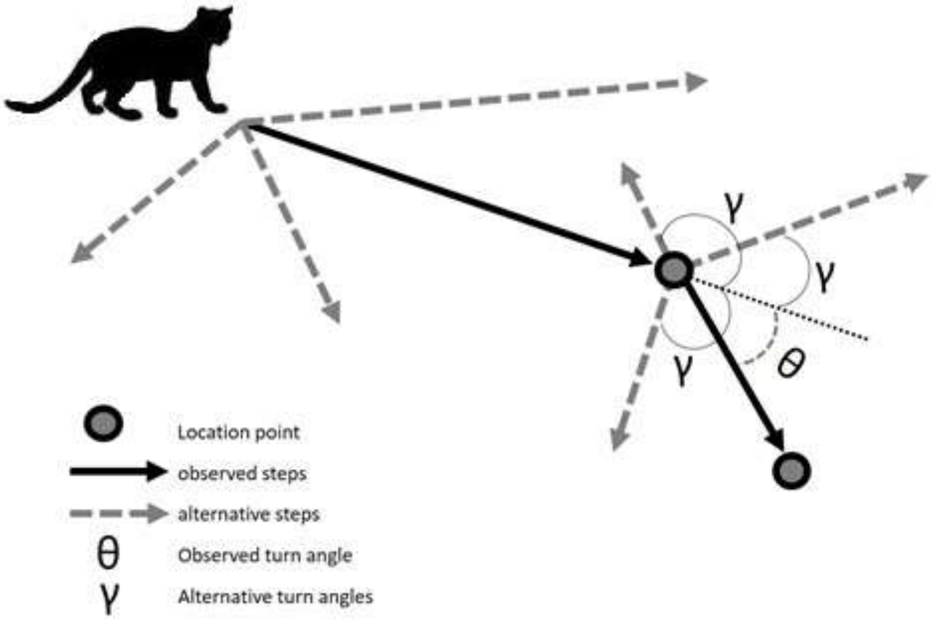

Fig. 2. Schematic representation of the deconstruction of animal trajectory in observed step (solid black lines) lengths and turn angles as well random alternative step (dotted grey lines) lengths and turn angles empirically parametrized, creating alternatives locations points to represent available habitats.

Therefore, to each step location of each individual, we have: time of day and type of habitat used. Using a Conditional Logistic Regression (CLR; following this matched case-control design), we compare used habitat (scored as 1) and available habitats (scored as 0) at each step performed by each individual (Fortin et al. 2005). The regression was logistic because its response variable is binary, represented by 1 (used habitat) and 0 (available habitats), and it is conditioned because used and available habitat are compared within each step. Time of day was including in CLR in interaction with the type of habitat as non-linear effects. Because the habitat selection varies cyclically along the day, we include it as trigonometric harmonics, which respects the circular nature of circadian time (sine [hour/2pi*24] and cosine [hour/2pi*24]). Thus, once fixed pasture as reference, the SSF takes the general form:

w[i,t,j] ~ f(

β_{1itj}* type of habitat +

β_{2itj}* type of habitat: sine [hour /2pi*24] +

β_{3itj}* type of habitat: cosine [hour /2pi*24];

where the function f was specified as exp(itj)/[1+exp(itj)] to assume the binomial distribution of residuals and, therefore, a logistic curve.

In the equation, w(ijt) represents the probability of use of the habitat i at time t by the individual j. The coefficient β_1 represents the strength of selection for forest habitats. The situation $\beta_1>0$ means that habitats are being selected (used above the available), whereas $\beta_1<0$ means that habitats are being avoided (used below the available) and β_1 values close to zero means that habitats are randomly used (used as available). In addition, β_2 and β_3 allow strength of selection for each habitat varying along the day. For assessing the individual heterogeneity of habitat selection among individuals and, then, to check for the generality of our full model, we rerun one SSF for each individual separately.

Finally, we estimated daily activity patterns by measuring the mean linear distances moved between fixes obtained on consecutive hours (see Pereira et al. 2006, Castillo et al. 2019). Thus, we used the Euclidean distance moved per hour as an index of activity level performed by an individual. And to describe the individual daily activity fluctuation we calculate the average moving distance per hour during the total tracking of each individual. During the sample tracking the sunrise and sunset varied between 5:27 – 6:06 hours am and 6:30 – 7:37 hours pm, respectively.

Results

Descriptive summary

We captured and collared 15 individuals of Geoffroy´s cat from February to November 2017 and tracked 14: three males and 11 females (Table 1). One individual was not found after recapture. The effort necessary to capture all individuals was 1080 trap-nights. By exception of three individuals (F2, F3 and F9) that presented the standard spotted coat, the remainder had a melanic fur. Two females (F1 and F4) were killed by domestic dogs during the monitoring period.

Table 1. Home range size (km^2) for 14 Geoffroy's cats *Leopardus geoffoyi* tracked in the Pampas ecoregion of Brazil. Total home ranges were estimated with Minimum Convex Polygon ($MCP_{100\%}$), Kernel ($K_{95\%}$) and Kernel Brownian Bridge ($KBB_{95\%}$). M: Males; F: Females. The table reports the interval of tracking, the days tracked, total location points (fixes) and body mass of each individual (weight, kg).

ID	Interval of tracking		Days	Fixes	Weight	$MCP_{100\%}$	$K_{95\%}$	$KBB_{95\%}$
F1	11-Apr-17	27-Jul-17	107	1237	2.50	1.628	1.382	1.667
F2	10-Jun-17	28-Sep-17	110	689	3.00	4.525	2.021	2.355
F3	03-Apr-17	27-Oct-17	207	2415	3.05	4.352	4.130	2.383
F4	28-Jan-17	31-Mar-17	62	635	3.00	3.130	2.365	1.714
F5	25-Mar-17	30-May-17	66	563	2.75	9.935	5.292	2.568
F6	27-Jan-17	01-Oct-17	247	2864	3.25	5.237	2.494	3.152
F7	06-Apr-17	29-May-17	53	605	2.75	0.992	0.582	0.779
F8	04-Feb-17	31-Mar-17	55	558	3.40	2.205	1.932	1.787
F9	23-Jun-17	30-Jul-17	37	414	3.00	3.398	1.259	0.660
F10	30-May-17	27-Oct-17	150	1773	3.05	5.386	3.070	1.708
F11	20-Jun-17	30-Jul-17	40	496	3.85	2.588	1.407	1.524
M1	29-May-17	01-Aug-17	64	689	5.50	14.462	20.087	13.482
M2	02-Feb-17	31-Mar-17	57	577	4.65	8.997	8.980	7.443
M3	08-Apr-17	27-May17	49	534	3.60	5.643	6.748	3.379

Home range

Individuals were tracked about 93 days (37-207 days), recording a mean of 1003 fixes (414 – 2864 fixes). Mean home range size (HR) for females were 2.24 km^2 (0.99 – 9.93 km^2; MCP), 2.53 km^2 (0.58 – 5.29 km^2; Kernel) and 2.09 km^2 (0.66 – 3.15 km^2; BRB). Mean HR for males were 9.70 km^2 (5.64 – 14.46 km^2; MCP), 11.94 km^2 (6.75 – 20.09 km^2; Kernel) and 8.10 km^2 (3.38 – 13.48 km^2; KBB) (Table 1, 2, Fig. 3).

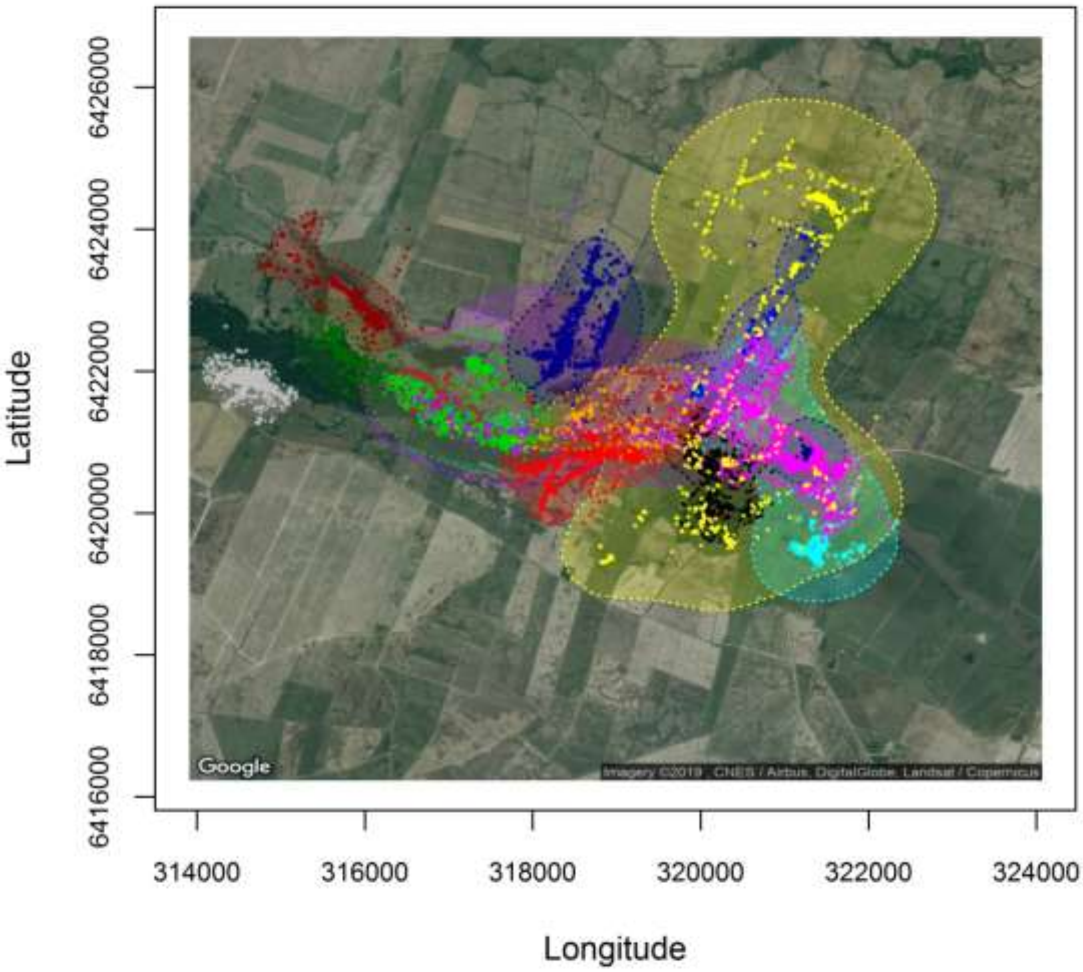

Fig. 3 – Overview of home ranges size (Kernel$_{95\%}$) of Geoffroy´s cat (*Leopardus geoffroyi*) in a human-modified habitat on southernmost Brazil. The colors represent each individual. Satellite image by Google Earth Pro©.

Table 2 – Geoffroy´s cat home range size (km^2) estimated in other areas of South America with fixes (mean; min - max) number and mean values of their respective estimators: Minimum Convex Polygon (MCP$_{100\%,\ 90\%}$) and Kernel (K$_{95\%}$). The Geoffroy´s cats were separated by number of individuals, sex (M: Males; F: female) and body size mass (Weight: mean weight, Kg; min – max or standard deviation, when available).

Reference	Country	Protected area	Sex	Weight	Fixes	MCP$_{100\%}$	MCP$_{90\%}$	K$_{95\%}$
Johnson & Franklin (1991)	Chile	Yes	4 F	4.2*	46.7 (33 – 61)	3.06 (1.35 – 5.16)	-	-
			5 M	4.8*	43.2 (22 – 62)	9.21 (3.92 – 12.41)	-	-
Manfredi et al. (2006)	Argentine	Yes	2 F	-	110/42	1.88 (2.43/1.34)	1.46 (1.97/0.96)	1.60 (1.86/1.35) **
			2 M	-	102/49	4.96 (5.03/4.90)	3.50 (2.72/4.29)	3.69 (3.08/4.31) **
Pereira et al. (2006)	Argentine	Yes	3 F	-	25.7 (23 – 28)	3.22 (1.3 – 6.23)	-	4.21 (2.17 – 6.18)
Castillo et al. (2008)	Argentine	No	1 M	6.6	40	26.96	-	28.77
Manfredi et al. (2012)	Argentine	No	1 F	-	135	-	6.1	4.87**
			2 M	-	54/110	-	4.98/7.2	7.67/9.28**
Pereira et al. (2012)	Argentine	Yes	2 F	2.88 ±0.35	19/35	0.47 (0.69/0.26)	-	-
			10 M	3.92 ±0.45	27 (18 – 42)	2.06 (4.00 – 0.61)	-	-
Pereira et al. (2012)	Argentine	No	2 F	2.88 ±0.35	31/23	2.92 (1.51/4.54)	-	-
			4 M	3.92 ±0.45	23.5 (19 – 27)	2.90 (2.20 – 4.00)	-	-
Tirelli et al. (2018)	Brazil	No	3 F	3.48 ± 0.35***	79 (35 – 133)	1.27 (0.86 – 2.06)	-	0.74 (0.21 – 1.03)
			4 M	4.63 ±0.57***	49.5 (23 – 62)	3.76 (1.13 – 7.90)	-	3.03 (1.02 – 7.04)
Castillo et al. (2019)	Argentine	No	3 F	3.23 (2.8 – 3.5)	37.3 (26 – 53)	1.13 (0.7 – 1.6)	-	0.83 (0.4 – 1.4)
			5 M	4.5 (3.8 – 6.7)	227.4 (55 – 414)	3.96 (0.4 – 6.6)	-	2.88 (0.4 – 5.5)
Mazim et al. (in submission)	Brazil	No	2 F	-	-	0.38 (0.19 – 0.57)	-	2.12 (1.81 – 2.43)
			7 M	-	-	1.79 (0.44 – 4.24)	-	3.81 (2.21 – 5.20)
This study	Brazil	No	11 F	3.05 (2.5 – 3.85)	1113.5 (414 – 2865)	4.23 (0.99 – 9.93)	-	2.53 (0.58 – 5.29)
			3 M	4.58 (3.6 – 5.5)	600 (534 – 689)	9.7 (5.64 – 14.46)	-	11.94 (6.75 – 20.09)

* mean weight value; ** K$_{90\%}$; *** estimated weight for 5 males and 5 females

Males home ranges were larger than females (t = -2.66; df = 13; p < 0.03) (Fig. 4). Both number of relocations (t = 0.77; df = 13; p = 0.46) and body mass did not caused a global effect on home range size (t = -0.28; df = 13; p = 0.78). However, the sex-body mass interaction indicated that larger males had larger home ranges while females did not varied home range size in according to body mass (t = 2.23; df = 13; p < 0.01) (Fig. 4). Larger home range for males was a consistent pattern among all reviewed studies on home range size of Geoffroy's cat (t = 5.17; df = 65; p < 0.01) (Fig. 5).

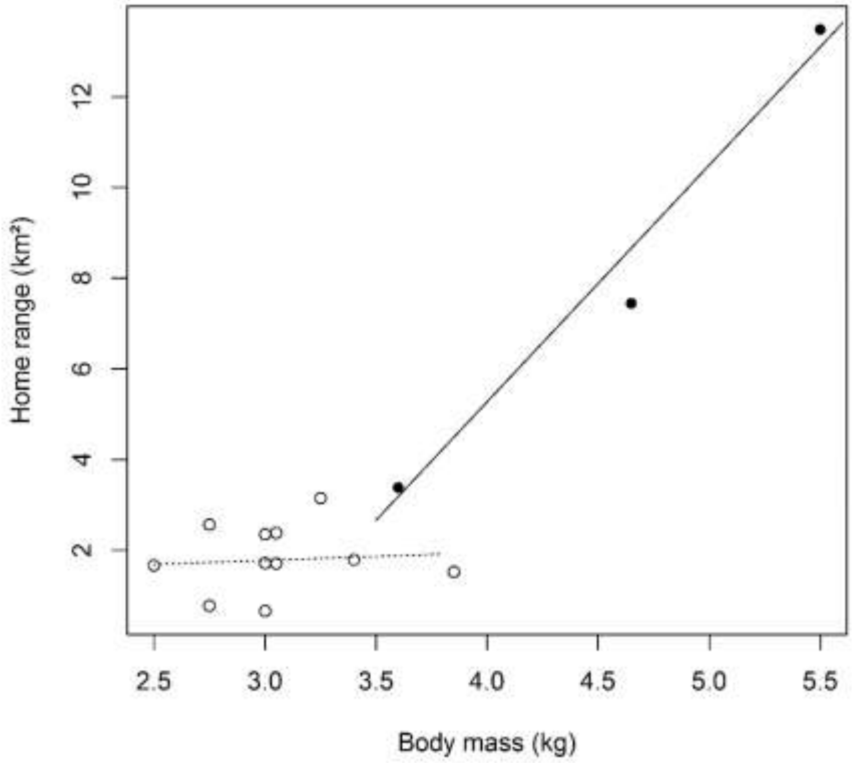

Fig. 4 – Sexual differences in the effect of body mass on home range size of Geoffroy´ cat. Males: black dots; Females: white dots. Lines depicts General Linear Model prediction for males (solid line) and females (dashed line).

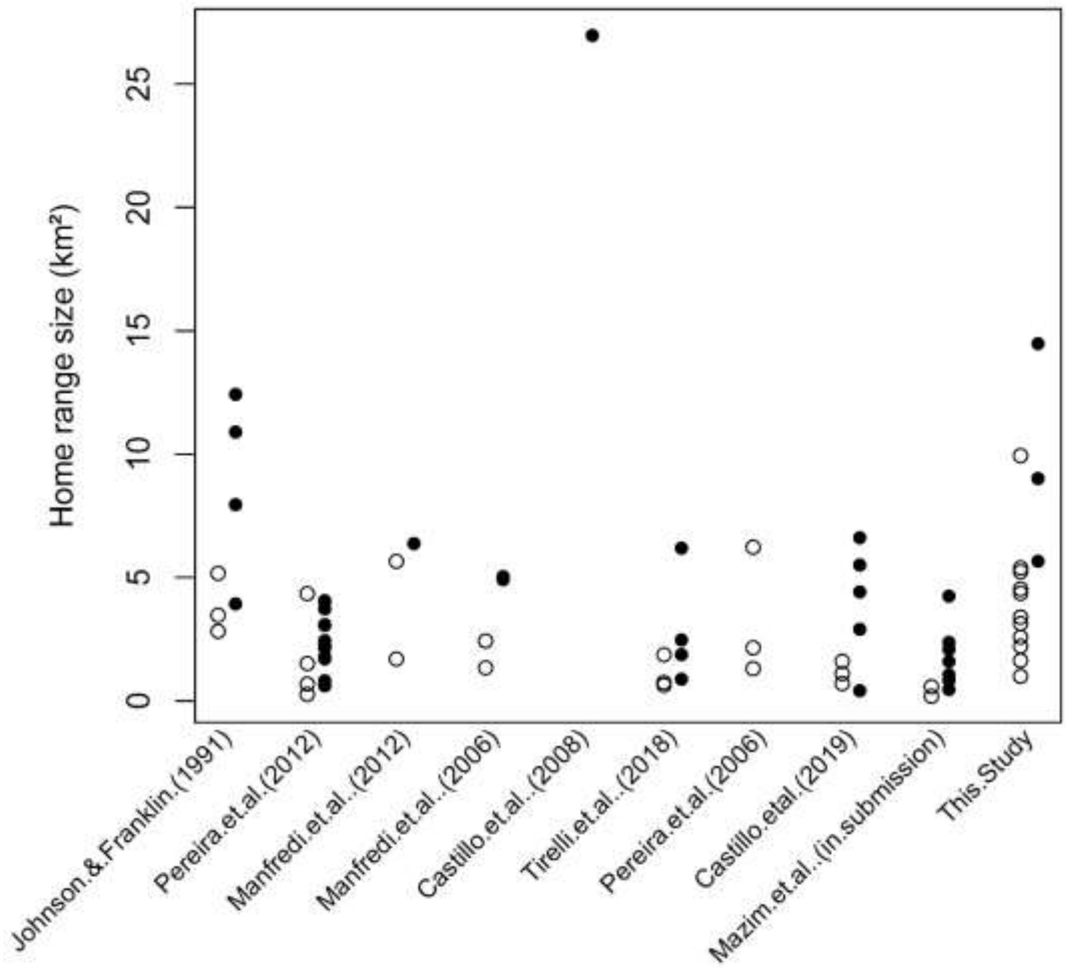

Fig. 5 - Geoffroy´s cat home range size (MCP, km^2) estimated at other areas of South America and the two tracking periods in our study area. Males: black dots; Females: white dots.

When we compared the size of the total area used by males and females of Geoffroy´s cat with the number sequence of relocations there is little evidence to suggest that total areas utilized by males were approaching asymptotic values (Fig. 6). This leads us to believe that the males had not yet exploited the total area of their territory before the end of our sampling. Contrary, females reached the asymptote even with few numbers of relocations. Asymptotes would be interpreted as possible maximum ranges.

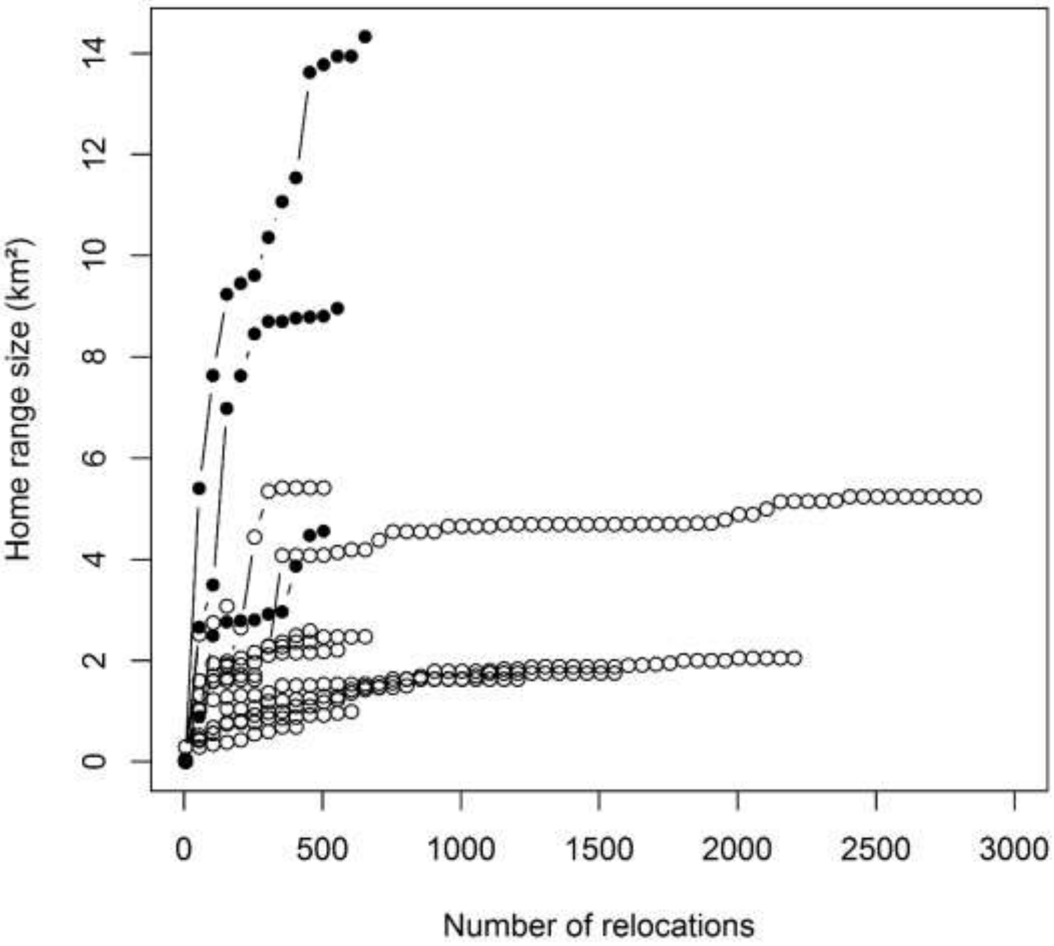

Fig. 6 - Size of the total area utilized by 14 adult Geoffroy´s cat (*Leopardus geoffroyi*) as a function of the number of relocations. Males: black dots; Females: white dots.

Habitat selection and activity pattern

Geoffroy´s cat exhibited nocturnal-crepuscular activity pattern (Fig. 7). Activity peaks began in the late afternoon, stabilizing during night and decreasing around sunset. Considering pasture as reference habitat, forest was the most selected at any time of day, mainly during daylight (Fig. 7). Water bodies, rice, roads and houses were avoided during daylight, but selected at dusk and first night hours. Althougth these habitats exhibit similar circadian shape of selection, water bodies and roads were usually more selected then rice and houses. Swamps presented opposite pattern to these last, being selected druing dayligth and avoided at nigth. Finally, pastures were avoided at all, except at morning when rice, roads and house were more avoided than it. When we assess individual heterogeneity of habitat selection (Fig. 8), we found a uniform selection for forest, water bodies and rice, but strong variability for road, swamp and house areas, which some individuals selected while others avoided the same habitat.

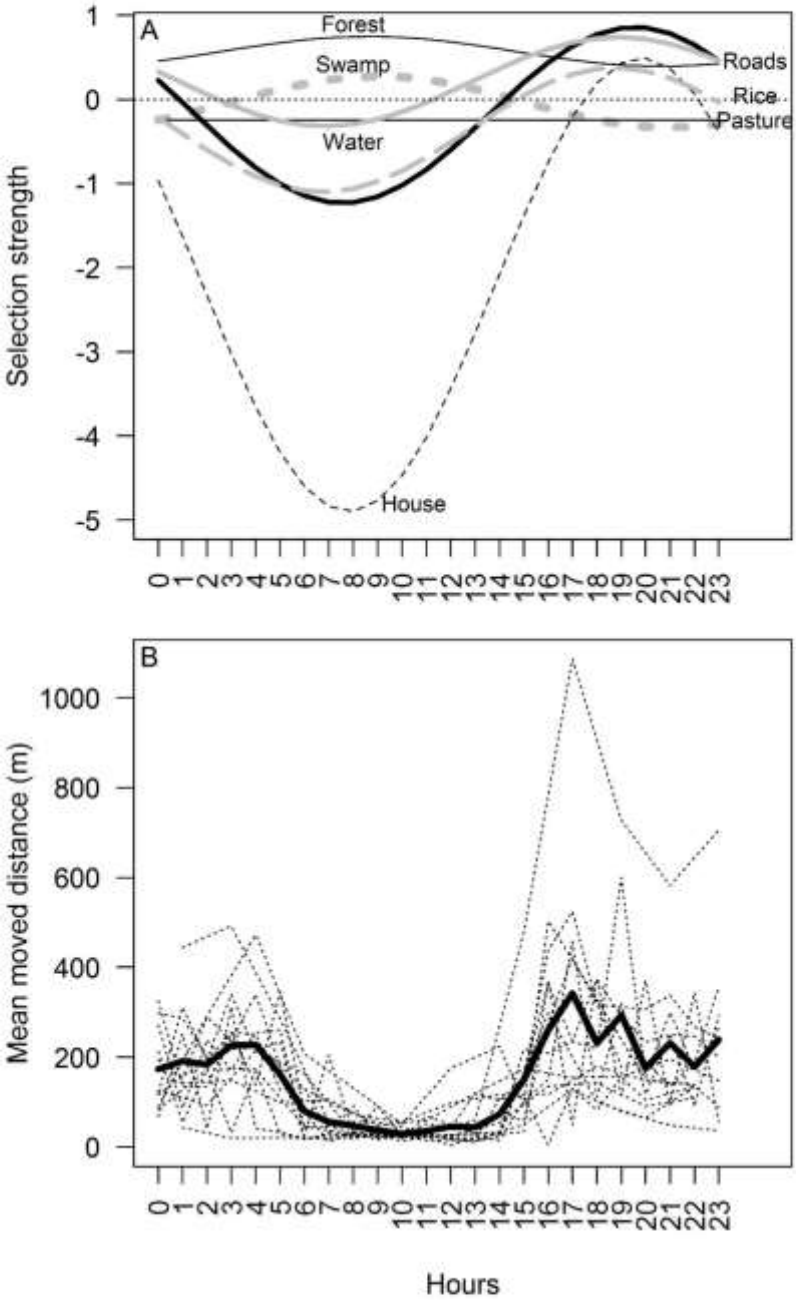

Fig. 7 - Graphical representation of the habitat selection and activity pattern by Geoffroy´s cat (*Leopardus geoffroyi*) at the daytime in a human-modified habitat on southernmost Brazil. Habitat selection (A): values below zero depict avoided habitat and above habitat selected. Values close to zero means that habitats are randomly used (smaller dotted line). Pasture was fixed as reference (solid black lines). Activity pattern (B): the dashed lines represent the mean moved distance for each individual and the black line the mean.

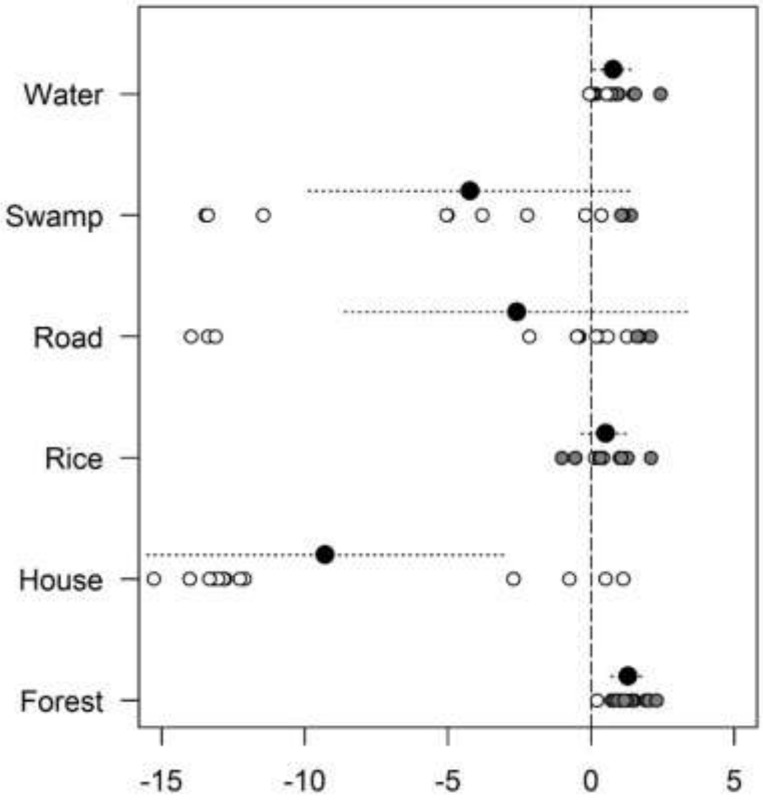

Fig. 8 - Graphical representation of individual heterogeneity of habitat selection of Geoffroy´s cat (*Leopardus geoffroyi*). Each small dot represents one individual, which gray dots indicate significant coefficients and white nonsignificant. Large black dots and whiskers depict population mean and standard deviation, respectively. Negative coefficient values depict habitat avoidance, positive values habitat selection, and values close to zero those habitats used in according to their availability (vertical dashed line).

Discussion

Our study presents refined Geoffroy´s cat tracking data that reinforces the hypothesis postulated in previous studies it exhibits tolerance to occupy human-modified habitats (Manfredi et al. 2006, Pereira et al. 2012, Tirelli et al. 2018). The selection for rice fields and farmhouses supports this statement. Despite its selection for disturbed areas, Geoffroy´s cat returned daily to riparian forests and other bodies of water, showing the importance of these habitats.

In general, our results show home range sizes are in disagreement with previous studies. Pristine habitats often lead to smaller home ranges size (see Pereira et al. 2012). This conclusion comes from human disturbances decreasing food abundance and heterogeneity, especially when cattle and horses are allowed to overgraze (e.g. Manfredi et al. 2012). Hence, our result area could be considered "pristine", since it rice fields and riparian forest kept the food abundance and heterogeneity. Our study area provides high abundance of small rodents and heterogenous habitat (prey capture success: 60% total and 90% in rice fields and swamp, Fábio D. Mazim, pers. comm; for regional small rodent diversity see Sponchiado et al. 2012, Quintela et al. 2013). As a result, we expected small home ranges in this area. However, we found home ranges with size as large as other disturbed areas. This apparent contradiction could be explained by to differences in the tracking method. Previous studies used VHF technology to track Geoffroy´s cat, which may underestimate home range sizes in disturbed environments (see Tirelli et al. 2008). In other words, if previous studies in disturbed environment would have used GPS technology, they would have found an home range larger than the one reported in our study. Data from Mazim et al. (in submission) for the same area support this assumption. The home ranges size is clearly smaller than those estimated by GPS, especially for males. Thus, despite of the ecological influences in the home ranges size variation, our study point that low home range values can be explained by limitation of the traditional telemetry.

When we compare home ranges size between genders, we have a consistent pattern across all available studies including our study. Males home ranges are larger than females. Tirelli et al. (2018) has demonstrated this pattern and suggest that the ecology of this felid is influenced by sexual selection. In general, males of other mammal species also have a larger home range than females (Gittleman & Harvey 1982). Males cover larger ranges to maximize the reproductive partners encounter, reassert its territory and provide their energetic needs (Beltrán & Delibes 1994, Carbone et al. 2007, Johnson et al. 2017). On the other hand, females perform smaller home ranges size due to their minor size and they have no stimuli to actively search for partners to reproduce (Gittleman & Harvey 1982). In addition, females exhibit tolerance in overlapping areas with other females, especially when genetically close (Tirelli et al. 2018). Therefore, our results reinforce the arguments of the Tirelli et al. (2018), where there is a strong influence of Geoffroy´s cat sex on home range size.

In general, our results showed a recurrent circadian pattern. During the daytime Geoffroy´s cat remains less active in the forests or water bodies edges and at night explores the surrounding open areas. Riparian forest is strongly selected by Geoffroy´s cat, most likely to provide an inconspicuous shelter (see Manfredi et al. 2006, 2012, Pereira et al. 2006). Geoffroy´s cat often found sleeping on trees or in log holes (José B. Soares, pers. comm.). Structurally complex habitats seem selected by Geoffroy´s cat in mosaic landscape context (Caruso et al. 2016, Tirelli et al. 2018, Castillo et al. 2019). These habitats also increase the chance of positive intra-specific interactions site by acting as an aggregating point for the individuals (Manfredi et al. 2006, Soler et al. 2009). Forests, however, do not seem to be provide more resources than other environments like water bodies edges or open habitats (Pereira et al. 2012). Thus, shelters seems to be the main attractor of forest environments.

The Geoffroy´s cat leaves the forest and water bodies edges in the late afternoon to feed in open areas. It uses the roads to explore the rice fields at night. Our results showed that Geoffroy´s cat display this general selection behavior for the edge of water bodies (small rivers, swamp or artificial canal). However, not every individual shared this tendency. Some individuals did not use the roads and rice fields at any time. Geoffroy´s cat explored the rice fields mainly for feeding (Sousa & Bager 2008, Kasper et al. 2016) and uses dry edges (dams) and their dirt road access as corridors. Another used habitat is the dry edges of channels, often formed by herbaceous plants and can concentrate semi-aquatic small mammals. Several fixes have been recorded over these linear edges. Therefore, this inconspicuous environment promotes a feeding ground and hideaway while in open areas and it must be a disputed or threatening habitat for some individuals.

Besides, we recorded Geoffroy´s cat in small bushes and planted forest patches, and even solitary trees in ranching and agricultural matrix may act as a shelter while exploring open modified habitats. But it seems to avoid lingering in planted areas for long, frequently returning for forest areas (see Andrade-Núñez & Aide 2010, Lantschner et al 2012). The ephemeral use of these ‘islands’ does not reduce their importance as an essential feature of the new habitat mosaic. The patches work as stepping-stones and increase the permeability of the matrix (Herrera et al. 2017). Other studies have also observed an analogous pattern (Manfredi et al. 2004, 2012, Pereira 2009, Soler et al. 2009). Caruso et al. (2016) suggests that the Geoffroy´s cat tolerate and occupy environments with human disturbance and fragmentation if shrublands are available (see also Manfredi et al. 2006, Pereira et al. 2011). These small islands (native or exotic) in the agropastoral matrix improve habitat heterogeneity and can help to maintain the cat in human-modified environments.

Some level of human-induced chances does not affect the Geoffroy´s cat activity patterns (Manfredi et al. 2011, Caruso et al. 2016), but daylight clearly increases the threats. Domestic dogs are serious risks during the day (see Pereira 2010). In our study area, almost all farmhouse has domestic dogs. They followed their owners during field work or when poaching. Two tracked individuals were killed by those dogs. Ranchers also hunt Geoffroy´s cat by retaliation of poultry predation, as described in other regions within the Pampas (Pereira 2010, Peters et al. 2016). Despite of all these threats, this small cat selected the farmhouses at nocturnal period, possibly attracted by poultry. This feeding behavior is well known for Neotropical small cats (Oliveira 1994, Tortato et al. 2013, Pereira 2010, Peters et al. 2016). That indicates that human disturbance is ambiguous; it can represent both risk but also great rewards for a foraging Geoffroy´s cat.

Predominantly nocturnal activity can be a consequence of the absence of larger size competitors (see Oliveira et al. 2010, Nagy-Reis et al. 2019). Larger nocturnal competitors could drive the Geoffroy´s cat to diurnal activities (see Oliveira-Santos et al. 2012). Beyond the current anthropogenic threats, it also shades they time and space with other carnivores, such as *Leopardus wiedii*, *Cerdocyon thous*, *Pseudalopex gimnocercus* (Kasper et al. 2012). But due the food abundance and similar body-mass of the potential competition does not seem to change the behavior of avoiding the overlap areas (see Gantchoff & Belant 2016). Another factor that could influence nocturnal activity is the synchrony of predator-prey activity (see Monterroso et al. 2013). *Cavia aperea* is the one of main prey to Geoffroy´s cat in southernmost Brazil (Sousa & Bager 2008) and display crepuscular activity (Asher et al. 2004). Other important prey have nocturnal habits (Sousa & Bager 2008, Paglia et al. 2012). Thus, the nocturnal-crepuscular activity must be firstly driven by synchronicity of the predator-prey activity, but seems reinforced by absence of larger competitors and daylight anthropogenic threats.

The mosaic of riparian forests, small shrubs patches, pastures and rice fields create a landscape structurally analogous to the original habitat. But, human-induced changes mainly affect the interactions between species and consequently the functional traits of the ecosystem (Grande et al. 2018). Extinctions by overhunting and replacement of native by exotic species are the clearest evidence of this functional disruption (Medan et al. 2011, Galiana et al. 2014). The lack of more specialized ecological interactions can lead to loss of the most exigent species (e.g. Fleming et al. 2014). From this perspective, there must be a maximum disturbance level to Geoffroy´s cat persistence in the new ecosystem. Though there is a record in an intensely human-modified area (Castillo et al. 2008), studies have already demonstrated that this specie use areas with low levels of human disturbance (Manfredi et al. 2006, Pereira et al. 2006, Lantschner et al. 2011, Caruso et al. 2019). Anthropogenic changes were not enough to locally extinguish this small carnivore in our study area. On the contrary, the Geoffroy´s cat population seems to have sufficient resources to remain. Despite being a rural area with constant human presence, we recognize three central drivers that counteract human threath: i) prey abundance and availability, ii) habitat structural complexity and iii) the absence of larger competitors (see Oliveira et al. 2010, Pereira et al. 2012). The trophic dynamics and absence of larger competitors are unlikely to change, but the fate of structural complexity is uncertain. The riparian forest is the most threatened and important natural habitat in or mosaic landscape area. Their depletion can have a major impact on Geoffroy´s cat populations.

General conclusions

Previous studies have demonstrated the Geoffroy´s cat adaptability in feeding and habitat use. By summarizing the different results of these studies, we can state that this is an adaptative response to the diversity of habitats it occupies.

Our meta-analysis showed that the diet flexibility can be extended to a large scale. The latitude, human disturbance and especially altitude are important drivers to Geoffroy´s cat diet across South America. It shifts prey-size following this biogeographic and anthropogenic changes. And the variation of prey abundance and availability in these gradients seems to be a determinant trait in large scale context. But despite all indirect effects of latitude, altitude and human disturbances on diet, the specialization was focused on larger prey. This should be linked to the recent human-induced changes, especially at lower altitudes.

In small scale, Geoffroy´s cat showed its adaptability by including human-modified habitats in its daily activities, even under anthropogenic threats. The home ranges size was as large as others disturbed environments, estimated in previous studies and the body-size variation between the sexes is decisive for any discussion of space use by this small cat. The refined data provided by the GPS technology enabled us to establish the dynamics of habitat selection in a landscape dominated by flooded rice fields and cattle pasture. Geoffroy´s cat uses the riparian forest and swamps intensely, especially at daylight. And at the nocturnal period it explores the rice field for it abundance of food. The few fragments of native forest and swamp patches have great value for Geoffroy´s cat conservation. Even with several anthropogenic threats, this mosaic context seems to improve the Geoffroy´s cat resilience in the human-modified landscape.

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