Taylor & Francis
Taylor & Francis Group

Studies on Neotropical Fauna and Environment

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/nnfe20

Small prey for small cats: the importance of prey-size in the diet of southern tiger cat *Leopardus guttulus* in a competitor-free environment

Marcos Adriano Tortato, Luiz Gustavo Rodrigues Oliveira-Santos, Maurício Osvaldo Moura & Tadeu Gomes de Oliveira

Taylor & Francis
Taylor & Francis Group

ORIGINAL ARTICLE

Small prey for small cats: the importance of prey-size in the diet of southern tiger cat *Leopardus guttulus* in a competitor-free environment

Marcos Adriano Tortato [a,*], Luiz Gustavo Rodrigues Oliveira-Santos [b], Maurício Osvaldo Moura [a] and Tadeu Gomes de Oliveira [c,d]

[a]Programa de Pós-Graduação em Ecologia e Conservação, Universidade Federal do Paraná, Setor de Ciências Biológicas, Curitiba, Brazil; [b]Instituto de Biociências, Universidade Federal do Mato Grosso do Sul, Campo Grande, Brazil; [c]Departamento de Biologia, Universidade Estadual do Maranhão, São Luís, Brazil; [d]Instituto Pro-Carnívoros, Atibaia, Brazil

ABSTRACT

Small cats can have a direct influence on the organization of small Neotropical vertebrate communities. However, the magnitude of influence and role(s) played by small felids, including *Leopardus guttulus*, in regulating prey populations is not well understood. This study aims to determine if there is a key-taxon in the dietary composition of the southern tiger (S-tiger) cat and evaluate the relationship between prey availability and use in the *restinga* habitat of Southern Brazil. *Oligoryzomys* spp. were identified as one of the main prey items and found to be among the highest density mammal species in the *restinga* habitat. However, as *Oligoryzomys* spp. were not among the preferred prey species in the S-tiger cat's diet, the high frequency of predation is probably a consequence of their high abundance. The diet of the S-tiger cat is characteristic of a generalist predator, eating a high diversity of different prey species, consumed per their availability, and selected according to mass and accessibility. However, in this area devoid of other felid competitors and with abundant prey, S-tiger cat seems to consume prey species within a relatively narrow mass spectrum (6–25 g), although it does not appear to select any specific taxon of any class size.

ARTICLE HISTORY
Received 2 July 2020
Accepted 8 March 2021

KEYWORDS
Atlantic forest; diet; electivity; *Oligoryzomys*; Serra do Tabuleiro State Park

Introduction

Due to their range of diet, body size, and tolerance for different physical environments, carnivores can act as key species in structuring communities (Finke & Denno 2005; Berger et al. 2008). Their role in community dynamics, potentially regulating prey density and that of other carnivore species, or even indirectly influencing plant communities, is being increasingly highlighted (Fonseca & Robinson 1990; Gittleman et al. 2001). Food availability is a primary determining factor in carnivore life-history, influencing patterns of habitat use, foraging strategies, and variations in behavior (Ewer 1973; Fonseca & Robinson 1990). However, understanding the dietary composition of carnivores is insufficient to elucidate their overall life-style. Understanding the biology of prey species and what determines how they are preyed upon is also insightful. Emmons (1987) noted that studies of the predator-prey relationships of carnivorous mammals are scarce and mostly restricted to the temperate zone. Although this observation was made in 1987, it remains valid, probably because of the difficulty of conducting such studies in more complex tropical communities.

Felids are hyper-carnivores, feeding exclusively on vertebrates (Ewer 1973), and are the top predator species in tropical forest habitats (Emmons & Feer 1997). In Brazil, the Family Felidae is represented by nine species (Kitchener et al. 2017), of which the southern tiger (S-tiger) cat, *Leopardus guttulus* (Hensel 1872), is among the smallest, with body proportions similar to that of a domestic cat (de Oliveira & Cassaro 2005; Figure 1). *Leopardus guttulus* was formerly regarded as a subspecies of *Leopardus tigrinus*, but was recently reclassified as a distinct species (Trigo, Schneider, et al. 2013). Although their distribution limits remain poorly defined, in Brazil, *L. guttulus* occurs in the south, southeast, and parts of the central region of the country (de Oliveira et al. 2016; Payan & de Oliveira 2016). *L. guttulus* is considered vulnerable in

CONTACT Marcos Adriano Tortato marcostortato@hotmail.com

*Present address: Rua Salvatina Feliciana dos Santos, n.155, Bairro Itacorubi, CEP 88034-600, Florianópolis, Santa Catarina, Brazil
Supplemental data for this article can be accessed here.

Published online 20 Jun 2021

Figure 1. Southern tiger cat *Leopardus guttulus* in the *restinga* of Serra do Tabuleiro State Park, southern Brazil.

Brazil and globally (MMA 2014; de Oliveira et al. 2016).

Tiger cats are poorly known (Sunquist & Sunquist 2002; de Oliveira 2006 and possess a myriad of intricate or unsolved biological and natural history features. These doubts include conflicting phylogenetic hypotheses and unclear geographic distributions, habitat use, population parameters, and interspecific relationships (see de Oliveira et al. 2010). Even though tiger cats are widely distributed and characterized by broad habitat usage, certain basic information, such as dietary composition, remains largely unknown.

As with other smaller felid species, the diet of tiger cats is primarily based on the consumption of birds, reptiles, and small mammals, in varying proportions (de Oliveira 1994; de Oliveira et al. 2010). Among all publications that refer to the S-tiger cat diet, we found only seven that provided any detailed information about the species feeding habits (Facure-Giaretta 2002; Wang 2002; Rocha-Mendes et al. 2010; Silva-Pereira et al. 2010; Rinaldi et al. 2015; Seibert et al. 2015; Nagy-Reis et al. 2019). The other studies were based on just a few samples (stomach contents and feces/scat) and showed a very gross pattern of feeding ecology (e.g. Facure & Giaretta 1996). One major drawback to achieving a clear understanding of how the S-tiger cat interacts with its prey is that, with two exceptions (Facure-Giaretta 2002; Silva-Pereira et al. 2010), there is no detailed information about prey availability. The limited knowledge we have of predator-prey relationships in small-medium sized tropical felids suggests that they are generalist predators (e.g. Sunquist & Sunquist 2002; de Oliveira et al. 2010).

Although prey availability is a key component to understanding predator-prey dynamics, the presence of other predator species can alter the dynamics of the whole system through synergistic or antagonistic cascading effects (Pettorelli et al. 2011). It is expected that under different conditions, such as with and without top predators or other potential competitors, the feeding dynamics of mesopredators should change. This is the scenario found in the *restinga* area of Serra do Tabuleiro State Park; the southern tiger cat is the only felid predator currently present (see Cherem et al. 2011). The other Carnivora in the *restinga*, the crab-eating fox (*Cerdocyon thous*) and the crab-eating raccoon (*Procyon cancrivorous*) are omnivores-frugivores, not hypercarnivores as felids are (de Oliveira & Pereira 2014), whereas the lesser grison (*Galictis cuja*) is virtually absent altogether (see Cherem et al. 2011). Hence, we assume there is no competitive pressure to influence S-tiger cat dietary composition and prey selection there. Because of this, we ask: is there a key taxon in the diet of the S-tiger cat? We also test the hypothesis that the S-tiger cat is a carnivore that does not select any specific prey taxon. This would allow the determination of what could be defined as the fundamental dietary niche of the species. From the perspective of food niche theory, we would expect southern tiger cat prey selection into the most profitable prey group. We also wanted to assess how the abundance of the most selected or potentially profitable prey could affect the species diet.

Material and methods

Study area

The study was conducted in Serra do Tabuleiro State Park (STSP), located in the east-central region of Santa Catarina State, southern Brazil. This is one of the largest protected areas in the region, covering approximately 85,000 hectares and ranging in elevation from sea level to 1250 m. STSP is part of the highly-threatened Atlantic Forest domain in Brazil and is considered the most important area for the worldwide conservation of S-tiger cat (de Oliveira et al. 2016). STSP is characterized by dense rainforests, mixed broadleaf Araucaria forests, montane grasslands, and a coastal area of mangroves and *restingas* (Klein 1981). The study site was located in the *restinga* habitat, a unique and varying coastal vegetation with small trees and dominated by dense shrubs on sandy soil, in STSP (27°49'39" – 27°49'34" S and 48°36'59" – 48°37'27" W; Figure 2).

According to the Köeppen system, the climate of the study site is humid mesothermal (Cfa), with hot summers. The average annual rainfall is around 1700 mm, and the average annual temperature is 20.5°C (16.3°C in July and 24.6°C in February). The *restinga* habitat at STSP consists predominantly of herbaceous and shrub

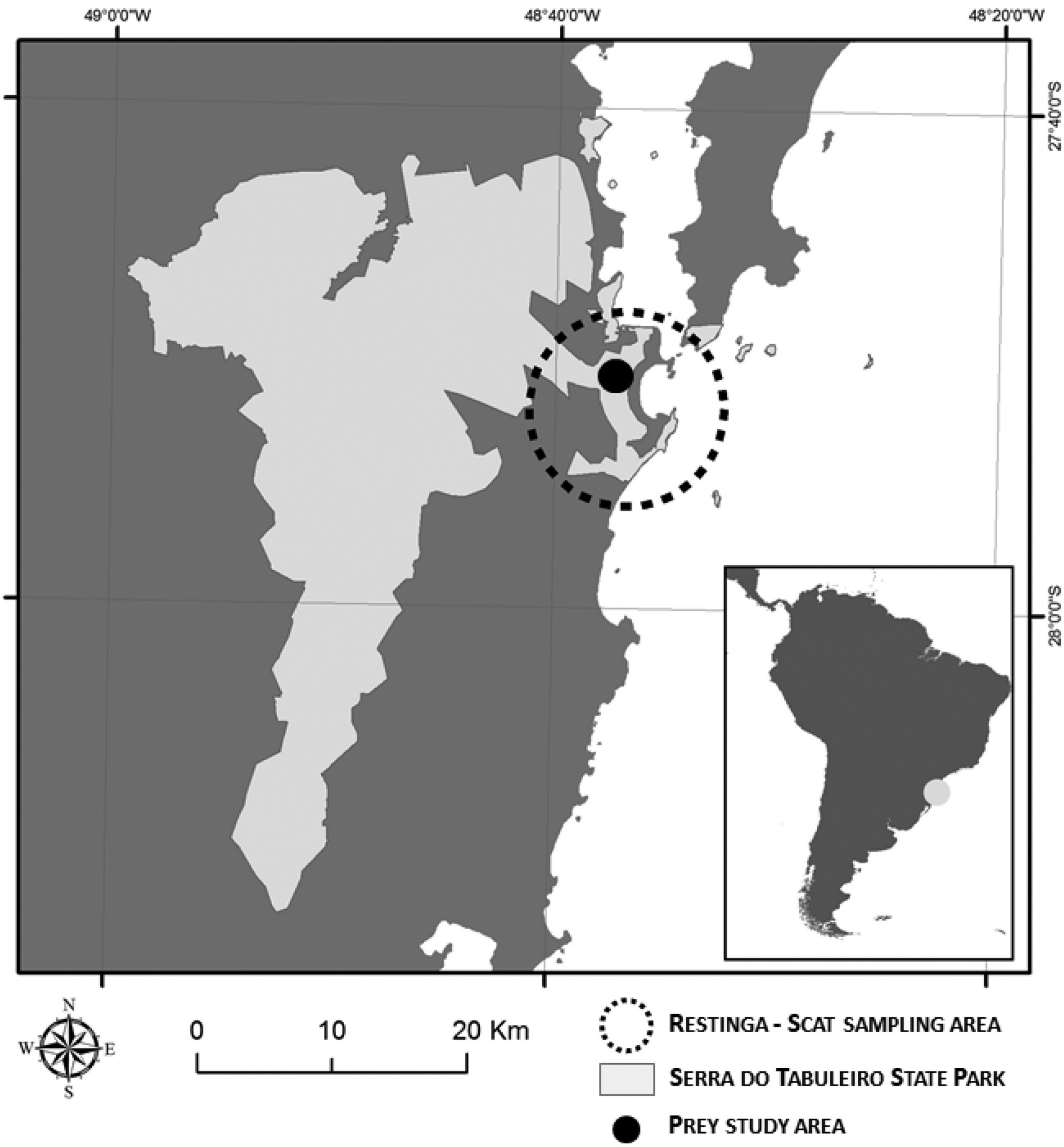

Figure 2. Location of the study area in the coastal plain of Serra do Tabuleiro State Park, Santa Catarina, Brazil.

vegetation with a few trees and shrubs in drier areas and on sandy ridges (Klein 1981).

Diet composition procedures

Fieldwork was conducted biweekly between December 2005 and December 2007. Scat samples were collected along four trails, in an area of approximately 40 km^2. Diet was determined by analyzing all of the animal remains that were recovered from southern tiger cat scat samples, following Quadros and Monteiro-Filho (2006a, 2006b). Expert taxonomists were consulted whenever necessary. Samples of feces with guard-hairs that either did not allow for predator confirmation or were not from S-tiger cat were discarded from the analysis. Identifications of prey items were made to the most specific taxonomic level possible, and the data were presented as the frequency of occurrence and relative frequency of prey items (Krebs 1999). The *G test* was used to determine if seasonal variation (summer, fall, winter, and spring) affected prey item frequency (Zar 1999).

Prey study

We also assessed the small non-volant vertebrates occurring in the fecal collection areas. Animals were captured using live traps and pitfalls with drift fences; they were weighed, tagged and released at the same point of capture (study license permits: FATMA/DEAM #001963, IBAMA/DIREC/SC #031/06, CENAP/IBAMA #054/04). Mammals and reptiles (lizards with legs) were marked with numbered metal tags; snakes and limbless lizards were individually marked by removing scales from different regions of their bodies. Live-traps were equally distributed in areas of open (mainly herbaceous) and dense (predominantly trees and shrubs) vegetation for a 5-day period each month. Pitfalls were installed in four 110 m long trap lines, 500 m apart. Each line consisted of ten buckets, or five 35-L and five 60-L buckets, spaced 10 m apart and in alternating positions by size (see Lyra-Jorge & Pivello 2001; Umetsu et al. 2006). Six additional trapping stations consisting of Y-shaped arrays were also installed at a distance of 500 m apart, with a bucket of 100 L per station. The trap line buckets were connected via 10 m long and 0.5 m high canvas guide fences or drift fence barriers. The three individual segments of each "Y" shaped trap line array were formed using guide fences of the same height and length, with a single bucket in the center. For the live-trap sampling, 75 units of various sizes (30 measuring 32 × 20 × 20 cm, 30 measuring 35 × 18 × 17 cm, and 15 measuring 40 × 20 × 19 cm) were baited using bananas smeared with peanut butter and spaced at a distance of 10 m apart. The Tomahawk style live-traps were placed randomly along four transects directly on the ground, and one transect in the understory at a height of 2–4 m. Each transect included 15 live-traps.

Electivity index and relative importance of each prey

Jacob's electivity index was used to determine the relationship between prey availability and use of prey, or rather, the quantitative importance of each item in the diet and environment (Jacobs 1974). This index is an adaptation from the *Ivlev Electivity Index* (Ivlev 1961). The Jacobs electivity index is calculated as: $D = (r-p)/(r + p-2rp)$, where r and p are the percentages of prey items in the diet and environment, respectively. The index ranges from −1 to +1, where a value of −1 means there is total avoidance of the feeding item, a value of zero signifies no preference and, a value of +1 represents a total preference for that food item by the cat. In this case, it is assumed that the term 'preference' refers to the electivity for a particular prey-item by the southern tiger cat. Furthermore, only prey items that were identifiable to at least the level of the genus were considered in the analysis. The electivity index was calculated for all fecal samples and also tested by season.

The index of relative importance (*IRI*), as suggested by Krebs (1999) and from Pinkas et al. (1971), was used to determine the relative importance of each prey item in the diet of S-tiger cat. After obtaining the *IRI*, each prey item was classified according to its order of importance in the southern tiger cat's diet, as follows: main items ($IRI > 50$), secondary items ($10 < IRI < 50$), and occasional items ($IRI < 10$). The body mass of each bird prey item was extracted from the literature (Belon 1994), and for all unidentified species, a mean weight for all Passeriformes was applied (15 g, see Belon 1994; Sick 1997).

Differences between the consumption of prey items with different masses, and the variation in consumption throughout the seasons, were analyzed using Pearson's chi-square test.

Results

Diet composition and prey selection

Of the 171 scat-samples collected, an average recovery rate of three samples per month, only 93 samples (54%) could be undeniably confirmed by guard-hair analysis as southern tiger cat feces, despite the observation of there being no other felid species in the area. In the *restinga*, S-tiger cat preys mainly on small mammals, birds, and reptiles, which represent 43.3%, 37.3%, and 16% of the relative frequency of its diet, respectively, according to the analysis of study sample contents. About 87% of the fecal samples had traces of mammals, 62% of birds, and 26% of reptiles.

We found an association between the frequency of predation by taxon and season (*Cramer* $C = 0.23$; $p = 0.01$; $n = 4$; $m = 3$). The significance of this relationship was likely influenced by a reduction in reptile prey following the summer season period (Supplemental Material, Figure S1).

Evidence for 20 identifiable prey items was recovered from the 93 focal species fecal samples (Table 1). Of these, 66 (71%) samples were necessary to reach a maximum number of dietary items. Except for the Brazilian marsh rat, *Holochilus brasiliensis*, all of the other mammal species captured in traps were also

Table 1. Dietary composition of southern tiger cats (*Leopardus guttulus*) in the *restinga* of Serra do Tabuleiro State Park, SC, Brazil, based on 93 fecal samples. N = number of individuals; FO (%) = frequency of occurrence; RF (%) = relative frequency; D = Jacobs' electivity index; IRI/Rk = index of relative importance/ranking of importance, M = mass (g).

Food Items	N	FO (%)	RF (%)	D	IRI/Rk	M (n)*
Mammalia						
Didelphidae						
Didelphis albiventris	2	2.1	1.36	0.498489	47.09/6	731.70 (4)
Marmosa paraguayana	6	6.4	4.15	0.322714	75.63/5	72.41 (52)
Cryptonanus sp.	7	7.5	5.0	0.427253	90.73/3	19.8 (11)
Monodelphis sp.	1	1.0	0.65	0.374311	2.15/12	19.0**
Unidentified Didelphidae	1	1.0	0.65	-	-	<20.0
Rodentia						
Oligoryzomys spp.	26	27.9	18.09	−0.14195	1212.85/1	17.63 (134)
Mus musculus	1	1.0	0.65	−0.08647	2.11/11	17.40 (3)
Euryoryzomys russatus	4	4.3	2.79	0.718712	34.75/8	56.05 (3)
Nectomys squamipes	3	3.2	2.07	0.54512	32.58/7	199.79 (4)
Unidentified Muridae	12	12.9	8.36			<20.0 (2)
Dasyprocta azarae	2	2.1	1.36	-	160.56/2	2800.0**
Squamata						
Ophiodes sp.	4	4.3	2.79	−0.39412	30.81/9	21.04 (6)
Mabuya dorsivittata	7	7.5	4.86	−0.38899	87.94/4	5.57 (10)
Colobodactylus taunayi	1	1.0	0.65	−0.77357	1.72/13	2.45 (5)
Unidentified Squamata	7	7.5	4.86	-	-	<10.0
Snakes	5	5.4	3.50	-	-	<100.0
Aves						
Anseriformes	1	1.0	0.65	-	-	<100.0
Charadriiformes						
Jacana jacana	2	2.1	1.36	-	15.45/10	155.0**
Passeriformes						
Sicalis flaveola	1	1.0	0.65	-	2.10/12	17.0**
Unidentified birds	51	54.8	35.53	-	-	15.0**
Insecta						
Coleoptera***	5	-	-	-	-	-

(*) Average mass of individuals captured in the field, (**) Mass according to Emmons & Feer (1997) for *D. azarae* and Belon (1994) for birds. For unidentified specimens, the mass of a similar, taxonomically close specimen was adopted; (***) Fragments or traces.

found in different proportions in the diets of S-tiger cats. Almost all of the fecal samples (92%) included grass (2–4 units), while Myrtaceae seeds were recovered from four samples (approximately 3%) (Table 1). Fragments of elytra beetles (Insecta) and one bird eggshell were also found in 5.4% and 1.1% of the samples, respectively. However, these items, as well as plant matter, were not considered as proper dietary items.

Although unidentified birds were the most consumed prey items, among identifiable species, pygmy rice rats (*Oligoryzomys* spp.) ranked first (18%). It was not possible to identify individual pigmy rice rat remains to the species level, but at least two species (*O. nigripes* and *O. flavescens*) were caught in pitfalls and Tomahawk style live-traps. It is also possible that some of the unidentified Murid specimens were actually some *Oligoryzomys* spp., as quite similar incisors and molars were found in seven out of 12 samples. However, these teeth samples could not be used to identify the species because they were either too fragmented or lacked any diagnostic features. Considering this uncertainty, it is possible that pigmy rice rats comprised more than 18% of the dietary items recovered here.

The fecal samples with identifiable traces of birds contained the remains of some Anseriform species, *Jacana jacana* and *Sicalis flaveola*. However, most of these samples were represented by feathers lacking pigmentation and broken or deteriorated in some way. Of all the bird samples, about 69% (n = 38) had small and new blood-feathers recently molted. The shape and size of most of these feathers indicated a predominance of small birds, with an estimated body mass of less than 20 g.

The seven samples of unidentified lizard remains were from small species, similar to the individuals caught in the pit trap array. Due to a lack of sufficient diagnostic features, none of the fecal samples containing snake scales could be identified with any degree of precision.

According to mass, very small-sized animals (< 20 g) were the most consumed prey items (Table 1), but larger-sized small prey (> 100 g) were also eaten. Interestingly, two fecal samples contained only hair and bones of the 'large-sized' Azara's agouti, *Dasyprocta azarae* (2.8 kg). However, given the length of the hair samples, they appear to be from young individuals that, nevertheless, would weigh ca. 1 kg.

The total field effort to determine the potential prey species of southern tiger cats in STSP consisted of 5625 live trap-nights and 3450 pitfall trap-nights, resulting in the capture of 4925 individuals representing three distinct taxonomic classes (Supplemental Material, Table S1). Six amphibian species, ten species of snakes and lizards, and ten mammals were identified, accounting for 90.35%, 8.35%, and 1.3% of the total trapping sample, respectively.

Amphibians were the most frequently trapped species, followed by mammals. Almost all the mammal trappings were of pigmy rice rats *Oligoryzomys* spp. In the *restinga* habitat, potential mammalian and reptilian prey species were captured more frequently in open areas (53.81%) than in dense vegetation (46.19%). Locomotor habits of both main and favored prey are terrestrial and scansorial (Supplemental Material, Table S2).

Electivity

The preferred prey of southern tiger cats were, in order of importance, Russet rice rat *Euryozyzomys russatus* (56 g), South American water rat *Nectomys squamipes* (200 g), white-eared opossum *Didelphis albiventris* (731 g), mouse opossum *Cryptonanus* sp. (20 g), short-tailed opossum *Monodelphis* sp. (19 g), and Tate's woolly mouse opossum *Marmosa paraguayana* (72 g) (Figure 3). Thus, the most favored prey species of *L. guttulus* were mainly larger-sized small mammals, even though they showed a low incidence of occurrence in the diet. The field mouse, *Mus muscuslus*, and the pygmy rice rat, *Oligoryzomys* spp. (both ca. 17 g) expressed low electivity for the southern tiger cats in STSP, the former ranking lower than the latter.

All lizard species were considered poorly elected prey-items by southern tiger cats, especially the Taunay Teiid, *Colobodactylus taunay*, which had the lowest electivity value of all prey items analyzed here.

Results of the Jacobs index analysis suggests that S-tiger cats preferred mammal prey with a body mass greater than 90 g and small marsupials (< 20 g), even though both prey items showed a low incidence of occurrence in the diet. According to the Jacobs index, the Russet rice rat (*Euryroryzomys russatus*) and South American water rat (*Nectomys squamipes*) prey species had the highest degree of selection, followed by small marsupials, white-eared opossum, *Didelphis albiventris*, mouse opossum, *Cryptonanus* sp., short-tailed opossum, *Monodelphis* sp., and Tate's woolly mouse opossum, *Marmosa paraguayana*.

When evaluating the electivity of prey by mass, those between 123 and 602 g were favored, and those weighing more than this were avoided (Figure 4).

Relative importance of each prey item

According to IRI, pygmy rice rats, *Oligoryzomys* spp., despite having the smallest body mass (17.63 g), were the most important prey item of southern tiger cats. The five main prey items, *Oligoryzomys* spp. *Dasyprocta azarae, Cryptonanus* sp., *Mabuya dorsivitatta*, and *Marmosa paraguayana* (Table 1) comprised

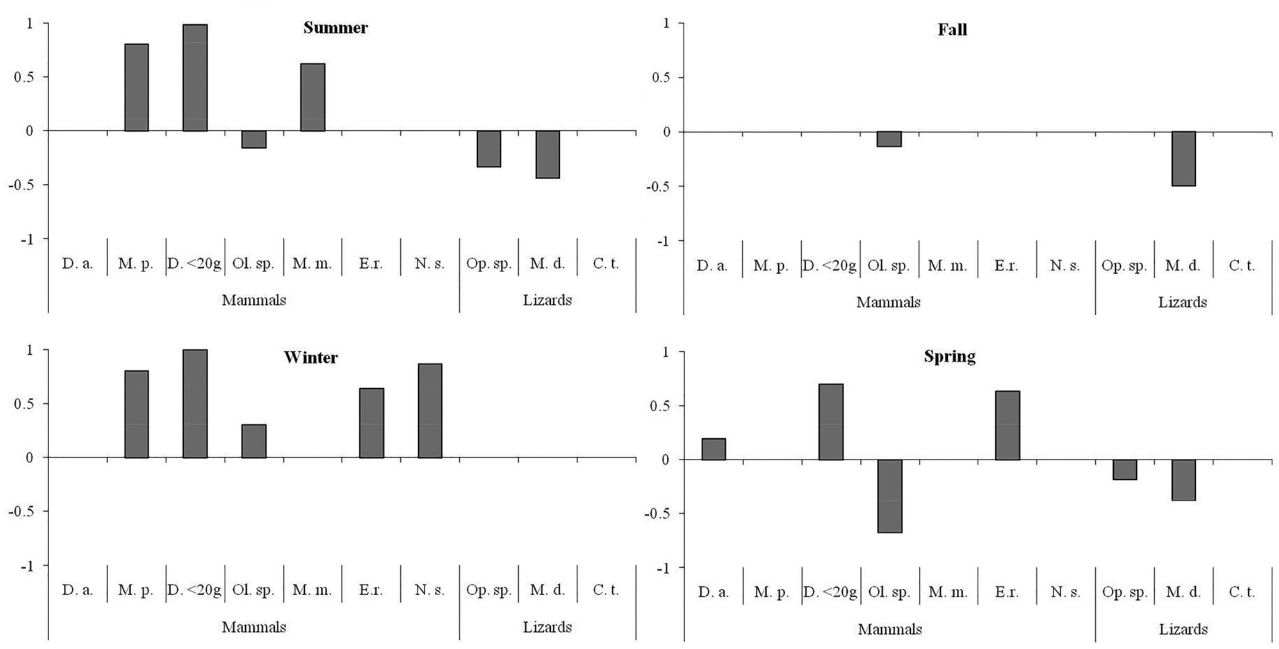

Figure 3. Seasonal electivity index of southern tiger cat, *Leopardus guttulus*, prey species in the *restinga* habitat of Serra do Tabuleiro State Park, SC, Brazil (0 value = electivity not rated). Da = *Didelphis albiventris*; Mp = *Marmosa paraguayana*; D. <20 g = Didelphidae <20 g; Ol.sp = *Oligoyzomys* sp.; Mm = *Mus musculus*; Er = *Euryoryzomys russatus*; Ns = *Nectomys squamipes*; Op.sp = *Ophiodes* sp.; Md = *Mabuya dorsivittata*; Ct = *Colobodactylus taunayi.*

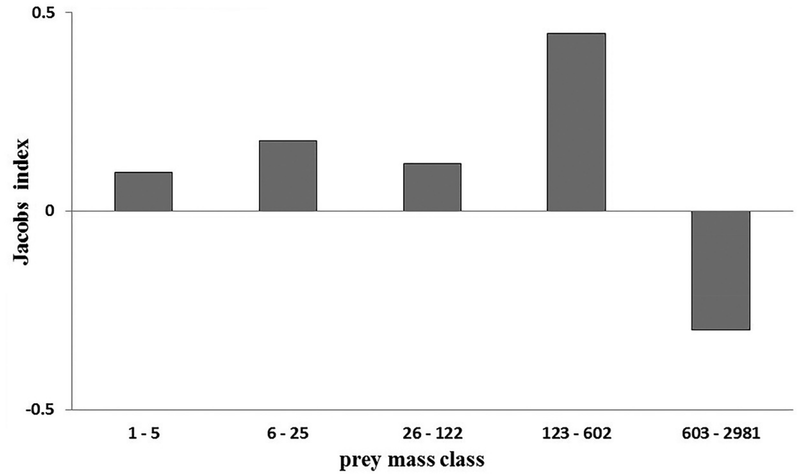

Figure 4. Electivity index of southern tiger cat (*Leopardus guttulus*) prey, grouped by mass class size, in the *restinga* of Serra do Tabuleiro State Park, SC, Brazil.

70.73% of the estimated total mass of the identifiable prey species and 63.31% of the total abundance. Except for *Oligoryzomys* spp., dense *restinga* is the preferred habitat of all these prey species (Emmons & Feer 1997; Eisenberg & Redford 1999; Reis et al. 2006). The secondary prey items amounted to 28.25% of the total mass observed in the diet, while the occasional items accounted for less than 1%. Abundance was probably the most important factor that contributed to the high *IRI* for *Oligoryzomys* spp., *Cryptonanus* sp., and *M. dorsivitatta*. In contrast, mass was probably the major determining factor in the *IRI* for *D. azarae* and *M. paraguayana* (Table 1). Interestingly, of the ten most important prey, five are among the top six selected species (Supplemental Material, Table S2). Also, the top three most important species had much higher abundance in the open *restinga*, whereas of the elected species, only *Cryptonanus* sp. was almost exclusively of the open *restinga*, all others were from the dense *restinga*.

An interesting pattern arises when all prey items are grouped according to mass-class size (Figure 5). The importance of prey weighing less than 25 g is evident (X^2 = 15.479, *d.f.* = 12, $P < 0.05$), even considering seasonal variation throughout the year. The differences in prey consumption by mass-class size are not influenced by the seasons (X^2 = 310.514, *d.f.* = 4, P = 0.216). This pattern somehow contrasts with the fact that the electivity index shows a much higher selection for larger prey (123–602 g size category) (Figure 4).

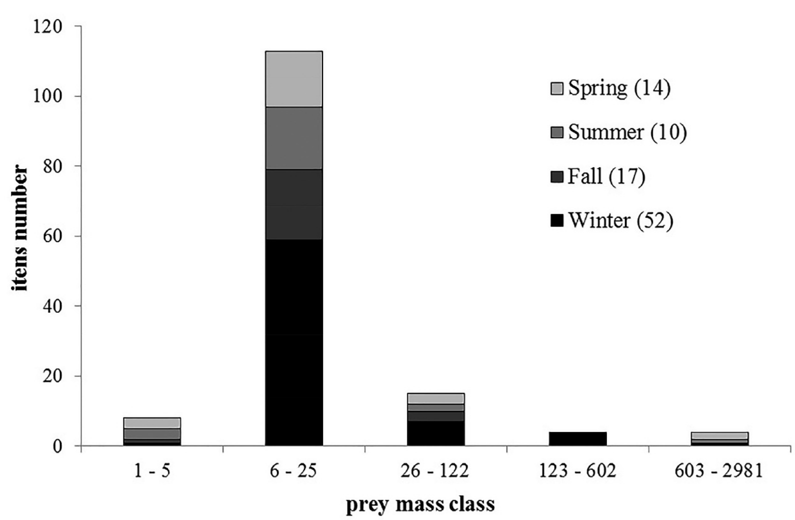

Figure 5. Total number of prey items consumed by southern tiger cats (*Leopardus guttulus*) at Serra do Tabuleiro State Park, grouped according to mass class size (Log scale).

Discussion

Diet composition and prey selection

The southern tiger cat diet at STSP was mainly based on the consumption of small mammals, with an important contribution from mammals having greater body mass (> 100 g) and birds. Reptiles were secondary prey items, but important during the warmer months of the year. Small mammals are commonly mentioned as a staple prey item, with birds and reptiles as secondary items (e.g. Facure-Giaretta 2002; Rocha-Mendes et al. 2010). Only one study reported a higher proportion of non-mammalian prey for the tiger cats' species complex (Olmos 1993), and this is currently the sole study of the northern tiger cat in Brazil. As such, there is as yet insufficient data to say that *L. tigrinus* and *L. guttulus* have different diets, and they likely exhibit the same patterns of consumption. Thus, although mammalian prey conforms to the norm, the relative proportions of birds and reptiles differed considerably in other studies (12.4% and 3.6% in Facure-Giaretta 2002; 29.6% and 2% in; Rocha-Mendes et al. 2010; 13% and 9.26% in; Nakano-Oliveira 2002; and 37% and 16% at STSP, respectively).

Birds have always been considered minor contributors to the dietary composition of the S-tiger cat (Facure-Giaretta 2002; Nakano-Oliveira 2002; Wang 2002; Rocha-Mendes et al. 2010). However, in the *restinga* habitat, birds not only accounted for nearly 40% of all prey items consumed, but they were also taken throughout the year. Although we cannot be certain about the birds eaten by S-tiger cats, the available evidence (feather structures and presence of pin feathers) suggests relatively small (< 20 g, e.g. *Sicalis flaveola*) or young/molting birds were eaten (Alatalo et al. 1984; Sullivan 1989).

The higher frequency of birds and reptiles in *restinga* is likely related to habitat structure, and thus, their accessibility and probability of being captured. It is expected that the regional diets of widely distributed species reflect the availability of different prey items throughout their area of distribution (see Arnold 1981; Delibes et al. 1997; Manfredi et al. 2004; Pereira et al. 2012). Indeed, this pattern has been seen for jaguars (*Panthera onca*), pumas (*Puma concolor*), ocelots (*Leopardus pardalis*), and Geoffroy's cats (*Leopardus geoffroyi*) throughout the Americas (see de Oliveira 2002; Manfredi et al. 2004; de Oliveira et al. 2010; Pereira et al. 2012).

Small lizards are not among the preferential dietary items of S-tiger cats in the *restinga*, even though they are abundant in this habitat. This might be due to the abundance of small mammals (de Oliveira 1994) in the area and the asynchronous activity periods of reptiles and S-tiger cat. Most reptiles are diurnal, whereas small mammals are mostly active at night, when southern tiger cats are also more active in STSP (Tortato & de Oliveira 2005). Thus, this pattern conforms to what has been reported elsewhere for the species (Facure-Giaretta 2002; Nakano-Oliveira 2002; Wang 2002; Rocha-Mendes et al. 2010). Although abundant in the *restinga*, amphibians were not identified as a component of the S-tiger cat's diet. The most prevalent prey taken (by both importance and electivity ranks) are very suggestive that *L. guttulus* uses intensely both the open and dense formations. Data on habitat use by this felid at the *restinga* of STSP corroborates this (Tortato & de Oliveira 2005; de Oliveira et al. 2008).

Electivity

Capture rate and electivity of prey types is influenced by their ease of capture and body size (Derting & Cranford 1989; Bisceglia et al. 2011). Additionally, differential prey vulnerability to predators, and hence selectivity, could be affected by their abundance, escape ability, microhabitat use, and activity period, which has been observed for Geoffroy's cat in Argentina (Bisceglia et al. 2011; Pereira et al. 2012). Thus, southern tiger cat selectivity for larger-sized small mammals might be related not only to prey size but also to their spatial use and locomotory habits. The small marsupial most frequently preyed upon in the *restinga*, the mouse opossum (*Cryptonanus* sp.), is typically considered to be an arboreal species (Paglia et al. 2012). However, in STSP, mouse opossums were captured at ground level, and this spatial usage pattern favors predation. The low electivity of Pygmy rice rats, *Oligoryzomys* spp. and the (alien) house mouse, *Mus musculus* might be related to their typically scansorial habits, especially the former species (Paglia et al. 2012). Although *Oligoryzomys* spp. were both the most abundant prey species in the environment and the most frequently consumed by southern tiger cats, they were not a preferred item in the diet, suggesting that their consumption is a function of abundance. Their consumption was also recorded by Rocha-Mendes et al. (2010) and Wang (2002), but not as the main dietary item, whereas Trigo, Tirelli, et al. (2013) found that *Oligoryzomys* spp. was the most important item for S-tiger cat in southernmost Brazil.

The low electivity of the three species of small lizards, as suggested by Jacobs' index, might be related to the reduced number of felid fecal samples collected during the warmer months of the year, which is also the period during which reptiles are most active. The low representation of reptiles could, in this way, be an underestimate because of the reduced availability of samples in the summer. Another possibility could be that this group does not represent the best source of energy gain within the region for southern tiger cats. Thus, our results would indeed be accurate. Reptiles have been shown as prominent only in the diet of the northern tiger cat in the semi-arid scrub habitat of the Brazilian *Caatinga*, where small mammals are scarse, and lizards abound (Olmos 1993).

It could be argued that the absence of other felid species in the *restinga* of STSP led to an expansion of the southern tiger cat's trophic niche. On the other hand, this assumption is unlikely, as it has been previously shown that the southern tiger cat diet did not suffer any dietary release in areas were the larger-sized ocelot was absent (de Oliveira et al. 2010). Thus, the consumption of larger-sized prey, such as white-eared opossum (*Didelphis albiventris*) and Azara's agouti (*Dasyprocta azarae*), should not be credited to the absence of larger-sized felids in the area. Consumption of larger prey (> 700 g) by this felid has been noted elsewhere (Facure-Giaretta 2002; Wang 2002; Rocha-Mendes et al. 2010). A similar pattern showing a numerical prevalence of small-sized prey, but with a much higher biomass contribution from the larger-sized part of the prey spectrum, has been highlighted in the ocelot diet throughout the Americas (de Oliveira et al. 2010).

The data suggest that prey selection by southern tiger cats at STSP is directed toward middle-sized small animals (> 50 g), especially mammals. However, the results clearly show that prey consumption is heavily concentrated on very small-sized prey (6–25 g), not on the preferred prey. We could speculate that this unexpected finding is simply a consequence of opportunistic feeding behavior, where the felid is taking advantage of the most abundant food resource. Alternatively, this could be a result of specialization for a certain size class of prey due to evolutionary food niche segregation with other conspecific small Neotropical felids, such as margay (*Leopardus wiedii*), jaguarundi (*Herpailurus yagouaroundi*), and ocelot, even though these felids are absent at the study site in STSP.

Relative importance of each prey

An interesting pattern that emerged from the dietary analysis of S-tiger cats at STSP is that, although it selects larger-sized prey, the bulk of its diet consisted of prey in the smallest size category. Therefore, pigmy rice rats (*Oligoryzomys* spp.) were the most important prey item, even though they had low electivity. Compared to other studies, equivalent-sized prey (ca. 20 g) also comprised the bulk of this felid's diet (Facure-Giaretta 2002; Wang 2002; Rocha-Mendes et al. 2010). This allows us to speculate that a preponderance of the smallest-sized prey in the diet of southern tiger cats is a result of resource partitioning with other species of small sympatric felids (*Leopardus* spp. and *Herpailurus yagouaroundi*). Nevertheless, the consumption of larger prey, such as the Azara's agouti, is also important for *L. guttulus* due to its biomass contribution. According to de Oliveira et al. (2008), very small (< 100 g) and larger (> 700 g) mammals contribute differently to the diet of this felid. The first contributes more numerically, while the second are more representative in terms of mass. The results of samples obtained in the *restinga* of STSP corroborate this.

Rocha-Mendes et al. (2010) found that S-tiger cat feeds on paca (*Cuniculus paca*) in a way that is similar to *D. azarae* in STSP. All other species of small Neotropical cats also take larger prey (de Oliveira et al. 2010). Nevertheless, the consumption of these larger-sized mammals should be considered occasional. Predation on this prey size category by small-sized felids is probably by adult males, young or sub-adults might contribute, as suggested by Ludlow and Sunquist (1987) for ocelots (11 kg) preying on the large-sized collared peccary (ca. 20 kg *Pecari tajacu*). Nevertheless, larger tiger cat individuals that can reach 3.5 kg (Sunquist & Sunquist 2002; de Oliveira et al. 2008) could indeed catch and handle adult prey items of around 2–4 kg, as has been previously noted (e.g. Leyhausen 1979). Moreover, the consumption of larger species might also be linked to the eventual consumption of carcasses. It is well known that felids, including Neotropical species, take advantage of this (Villa-Meza et al. 2002; Abreu et al. 2008).

Concluding remarks

The current study showed a rather interesting pattern of prey use by the southern tiger cat. Although larger-sized prey items (123–602 g) were selected, the smallest size category (6–25 g) was, by far, the most commonly taken. Prey is consumed according to availability and abundance, and is selected based on a combination of accessibility and larger body mass. We did not detect a key-taxon, but rather a prevalence of the class-size category of prey in the diet of the southern tiger cat. The pattern that emerges is that of an opportunistic, but specialized felid that, although preferring larger prey, is concentrating its hunting efforts on the most readily available resources in the area. Could the massive representation of very small prey be a matter of evolutionary ecological segregation with ocelots, margays, and jaguarundis, or simply a result of its opportunistic predatory habits? Further studies comparing small Neotropical felid diets could shed more light on this matter.

Acknowledgments

We thank Renê C. da Silva, Carlos J. de Carvalho Pinto, Jorge J. Cherem, Lauro C. Narciso, Hugo B. Mozerle, Javier Pereira, Luiz F. Pimenta and Jason Mobley for their contributions to this study. We thank Lamaq/UFSC, Instituto Pró-Carnívoros and CAPES (Brazil) for the scholarship to M.A. Tortato.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work was supported by the Brazil's National Environmental Fund (FNMA) under Grant 001/04 with additional support from Santa Catarina Environmental Institute (IMA) and CAIPORA Cooperativa.

ORCID

Marcos Adriano Tortato http://orcid.org/0000-0003-4928-5150
Luiz Gustavo Rodrigues Oliveira-Santos http://orcid.org/0000-0001-9632-5173
Maurício Osvaldo Moura http://orcid.org/0000-0001-7948-2986
Tadeu Gomes de Oliveira http://orcid.org/0000-0002-8760-3159

References

Abreu, K.C., Moro-Rios, R.F., Silva-Pereira, J.E., Miranda, J.M., Jablonski, E.F., & Passos, F.C. (2008). Feeding habits of ocelot (*Leopardus pardalis*) in Southern Brazil. Mammalian Biology, 73(5), 407–411

Alatalo RV, Gustafsson L, Lundbkrg A. 1984. Why do young passerine birds have shorter wings than older birds? Ibis. 126:410–415.

Arnold SJ. 1981. The microevolution of feeding behavior. In: Karnil AC, Sargent TD, editors. Foraging behavior: ecological, ethological, and physiological approaches. New York and London: Garland STPM Press. p. 409–453.

Belon W. 1994. Aves do Rio Grande do Sul: distribuição e biologia. São Leopoldo (Rio Grande do Sul, Brazil): UNISINOS Press.

Berger KM, Gese EM, Berger J. 2008. Indirect effects and traditional trophic cascades: a test involving wolves, coyotes, and pronghorn. Ecology. 89(3):818–828.

Bisceglia SBC, Pereira JA, Teta P, Quintana RD. 2011. Rodent selection by Geoffroy's cats in a semi-arid scrubland of central Argentina. J Arid Environ. 75:1024–1028.

Cherem JJ, Graipel ME, Tortato MA, Altoff S, Brüggemann F, Matos J, Voltolini JC, Freitas RR, Illenseer R, Hoffmann F, et al. 2011. Mastofauna terrestre do Parque Estadual da Serra do Tabuleiro, Estado de Santa Catarina, sul do Brasil. Biotemas. 24:73–84.

de Oliveira TG. 1994. Neotropical Cats, ecology and conservation. São Luis (Maranhão, Brazil): EDUFMA.

de Oliveira TG. 2002. Comparative feeding ecology of the jaguar and puma in the Neotropics. In: Medellín RA, Equihua C, Chetkiewicz CLB, Crawshaw Jr. PG, Rabinowitz A, Redford KH, Robinson JG, Sanderson EW, Taber AB, editors. El jaguar en el nuevo milenio. México (DF) and New York: Univ. Nac. Aut. México and Wildlife Conservation Society. p. 265–288.

de Oliveira TG. 2006. Research in terrestrial Carnivora from Brazil: current knowledge and priorities for the new millennium. In: Morato RG, Rodrigues FHG, Eizirik E, Mangini PR, Azevedo FCC, Marinho-Filho J, editors. Manejo e conservação de carnívoros neotropicais. São Paulo (Brazil): Edições IBAMA. p. 39–45.

de Oliveira TG, Kasper CB, Tortato MA, Marques RV, Mazim FD, Soares JBG, Schneider A, Pinto PT, de Paula RC, Cavalcanti GN, et al. 2008. Aspectos da ecologia e conservação de Leopardus tigrinus e outros felinos de pequeno-médio porte no Brasil. In: de Oliveira TG, editor. Estudos para o Manejo de *Leopardus tigrinus*/Plano de ação para conservação de *Leopardus tigrinus* no Brasil. Final report. Atibaia (SP, Brazil): Instituto Pró-Carnívoros/Fundo Nacional do Meio Ambiente. p. 37–105.

de Oliveira TG, Tortato MA, Silveira L, Kasper CB, Mazim FD, Lucherini M, Jácomo AT, Soares JBG, Marques RV, Sunquist ME. 2010. Ocelot ecology and its effect on the small-felid guild in the lowland Neotropics. In: MacDonald DW, Loveridge A, editors. Biology and conservation of wild felids. Oxford (UK): Oxford University Press. p. 559–580.

de Oliveira TG, Cassaro K. 2005. Guia de campo dos felinos do Brasil. São Paulo (Brazil): Instituto Pró-Carnívoros /Fundação Parque Zoológico de São Paulo/Sociedade de Zoológicos do Brasil/Pró-Vida Brasil.

de Oliveira TG, Pereira JA. 2014. Intraguild predation and interspecific killing as structuring forces of carnivoran communities in South America. J Mamm Evol. 21:427–436.

de Oliveira TG, Trigo T, Tortato MA, Paviolo A, Bianchi R, Leite-Pitman MRP. 2016. *Leopardus guttulus*. The IUCN Red List of Threatened Species 2016: e.T54010476A54010576. [cited 2017 Apr 12]. Available from: http://dx.doi.org/10.2305/IUCN.UK.2016-2.RLTS.T54010476A54010576.en

Delibes M, Blazquez MC, Rodriguez-Estrella R, Zapata SC. 1997. Seasonal food habits of bobcats (*Lynx rufus*) in subtropical Baja California Sur, Mexico. Can J Zool. 74:478–483.

Derting TL, Cranford JA. 1989. Physical and behavioral correlates of prey vulnerability to barn owl (*Tyto alba*) predation. Am Midl Nat. 121:11–20.

Eisenberg JF, Redford KH. 1999. Mammals of the neotropics. Vol. III. Chicago (IL): University of Chicago Press.

Emmons LH. 1987. Comparative feeding ecology of felids in a neotropical rainforest. Behav Ecol Sociobiol. 20:271–283.

Emmons LH, Feer F. 1997. Neotropical rainforest mammals: a field guide. Chicago (IL): The University of Chicago Press.

Facure KG, Giaretta AA. 1996. Food habits of carnivores in a coastal Atlantic forest of southeastern Brazil. Mammalia. 60:499–502.

Facure-Giaretta KG. 2002. Ecologia alimentar de duas espécies de felinos do gênero *Leopardus* em uma floresta secundária no sudeste do Brasil [PhD thesis]. Campinas (São Paulo, Brazil): Universidade Estadual de Campinas.

Finke DL, Denno RF. 2005. Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. Ecol Lett. 8:1299–1306.

Fonseca GAB, Robinson JG. 1990. Forest size and structure: competitive and predatory effects on small mammal comunities. Biol Conserv. 53:265–294.

Gittleman JL, Funk SM, Macdonald D, Wayne RK. 2001. Carnivore conservation. Cambridge (UK): Cambridge University Press.

Ivlev VS. 1961. Experimental ecology of the feeding of fishes. New Haven (Connecticut): Yale University Press.

Jacobs J. 1974. Quantitative measurement of food selection. Oecologia. 14:413–417.

Kitchener AC, Breitenmoser-Würsten C, Eizirik E, Gentry A, Werdelin L, Wilting A, Yamaguchi N, Abramov AV, Christiansen P, Driscoll C, et al. 2017. A revised taxonomy of the Felidae. The final report of the Cat Classification Task Force of the IUCN/SSCC at Specialist Group. Cat News Special. 11:80.

Klein MR. 1981. Fisionomia, importância e recursos da vegetação do Parque Estadual da Serra do Tabuleiro. Sellowia. 33:5–54.

Krebs CJ. 1999. Ecological methodology. Menlo Park (New York, USA): Addison Wesley Educational Publishers.

Leyhausen P. 1979. Cat behavior. New York (USA): Garland STPM.

Ludlow ME, Sunquist ME. 1987. Ecology and behavior of ocelots in Venezuela. Nat Geo Res. 3:447–461.

Lyra-Jorge MC, Pivello VR. 2001. Combining live trap and pitfall to survey terrestrial small mammals in savanna and forest habitats, in Brazil. Mammalia. 65:524–530.

Manfredi C, Lucherini M, Canepuccia A, Casanave E. 2004. Geographical variation in the diet of Geoffroy's cat (*Oncifelis geoffroyi*) in pampas grassland of Argentina. J Mammal. 85(6):1111–1115.

MMA. 2014. Espécies da fauna brasileira ameaçadas de extinção. Ministério do Meio Ambiente. Instrução Normativa n° 34, de 17 de outubro de 2013, Diário Oficial da União 18/10/2013, Seção 1, pág. 93. Portaria MMA nº 444/2014.

Nagy-Reis MB, Iwakami VHS, Estevo CA, Setz EZF. 2019. Temporal and dietary segregation in a neotropical small-felid assemblage and its relation to prey activity. Mamm Biol. 95:1–8.

Nakano-Oliveira E. 2002. Ecologia Alimentar e Área de vida de Carnívoros da Floresta Nacional de Ipanema, Iperó, SP (Carnivora: Mammalia). [PhD thesis]. Campinas (São Paulo, Brazil): Universidade Estadual de Campinas.

Olmos F. 1993. Notes on the food habits of Brazilian Caatinga carnivores. Mammalia. 57:126–130.

Paglia AP, Fonseca GAB, Rylands AB, Herrmann G, Aguiar LMS, Chiarelllo AG, Leite YLR, Costa LPC, Siciliano S, Kierulff MCM, et al. 2012. Annotated checklist of Brazilian mammals, 2nd ed. Occasional Pap Conserv Biol. 6:1–76.

Payan E, de Oliveira TG. 2016. *Leopardus tigrinus*. The IUCN Red List of Threatened Species 2016: e.T54012637A50653881. [cited 2017 Apr 12]. Available from: http://dx.doi.org/10.2305/IUCN.UK.2016-2.RLTS.T54012637A50653881.en

Pereira JA, Walker RS, Novaro AJ. 2012. Effects of livestock on the feeding and spatial ecology of Geoffroy's cat. J Arid Environ. 76:36–42.

Pettorelli N, Coulson T, Durant SM, Gaillard J-M. 2011. Predation, individual variability and vertebrate population dynamics. Oecologia. 167:305–314.

Pinkas L, Oliphant MS, Iverson ILK. 1971. Food habits of albacore, bluefin tuna and bonito in California waters. Calif Dept Fish Game Fishery Bull. 152:105.

Quadros J, Monteiro-Filho E. 2006a. Coleta e preparação de pêlos de mamíferos para identificação em microscopia óptica. Rev Bras Zool. 23(1):274–278.

Quadros J, Monteiro-Filho E. 2006b. Revisão conceitual, padrões microestruturais e proposta nomenclatória para os pêlos-guarda de mamíferos brasileiros. Rev Bras Zool. 23(1):279–292.

Reis NR, Peracchi AL, Pedro WA, Lima IP. 2006. Mamíferos do Brasil. Londrina (Paraná, Brazil): UEL.

Rinaldi AR, Rodriguez RH, Carvalho AL, Passos FC. 2015. Feeding of small neotropical felids and trophic nichoverlap in antropized mosaic landscape, South Brazilian. Biotemas. 28(4):155–168.

Rocha-Mendes F, Mikich SB, Quadros J, Pedro WA. 2010. Feeding ecology of carnivores (Mammalia, Carnivora) in Atlantic forest remnants, southern Brazil. Biota Neotropica. 10(4):21–30.

Seibert JB, Oliveira D de, Mendes S, Gatti A. 2015. Diet of two sympatric felids (*Leopardus guttulus* and *Leopardus wiedii*) in remnant of Atlantic forest, in the montane region of Espirito Santo, southeastern Brazil. Bol. Mus. Biol. Mello Leitão. 37:193–200.

Sick H. 1997. Ornitologia Brasileira. Rio de Janeiro (Brazil): Nova Fronteira Press.

Silva-Pereira JE, Moro-Rios RF, Bilski DR, Passos FC. 2010. Diets of three sympatric Neotropical small cats: food nicheoverlap and interspecies differences in prey consumption. Mamm Biol. 76:308–312.

Sullivan KA. 1989. Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaenotus*). J Anim Ecol. 58:275–286.

Sunquist M, Sunquist F. 2002. Wild cats of the world. Chicago (IL, USA): The University of Chicago Press.

Tortato MA, de Oliveira TG. 2005. Ecology of the Oncilla (*Leopardus tigrinus*) at Serra do Tabuleiro State Park, Southern Brazil. Cat News. 42:28–30. Cat Specialist Group, Muri.

Trigo TC, Schneider A, de Oliveira TG, Lehugeur LM, Silveira L, Freitas TRO, Eizirik E. 2013. Molecular data reveal complex hybridization and a cryptic species of neotropical wild cat. Curr Biol. doi:10.1016/j.cub.2013.10.046.

Trigo TC, Tirelli FP, Machado LF, Peters FB, Indrusiak CB, Mazim FD, Sana D, Eizirik E, Freitas TRO. 2013. Geographic distribution and food habits of *Leopardus tigrinus* and *L. geoffroyi* (Carnivora, Felidae) at their geographic contact zone in southern Brazil. Stud Neotrop Fauna Environ. 48 (1):56–67.

Umetsu F, Naxara L, Pardini R. 2006. Evaluating the efficiency of pitfall traps for sampling small mammals in the neotropics. J Mammal. 87(4):757–765.

Villa-Meza A, Meyer EM, Lopes-Gonzales CA. 2002. Ocelot (*Leopardus pardalis*) food habits in a tropical deciduous forest of Jalisco, Mexico. Am Midl Nat. 148(1):146–154.

Wang E. 2002. Diets of ocelots (*Leopardus pardalis)*, margays (*Leopardus wiedii)*, and oncillas (*Leopardus tigrinus*) in the Atlantic rainforest in southeast Brazil. Stud Neotrop Fauna Environ. 37(3):207–212.

Zar JH. 1999. Biostatistical analysis. New Jersey (USA): Prentice Hall.